PB83-189365

Submerged Aquatic Vegetation Distribution and Abundance in the Lower Chesapeake Bay and the Interactive Effects of Light, Epiphytes and Grazers

Virginia Inst. of Marine Science
Gloucester Point

Prepared for

Environmental Protection Agency
Annapolis, MD

Apr 83

U.S. Department of Commerce
National Technical Information Service
NTIS

EPA-600/3-83-019
April 1983

PB83-139365

SUBMERGED AQUATIC VEGETATION: DISTRIBUTION AND ABUNDANCE IN THE LOWER CHESAPEAKE BAY AND THE INTERACTIVE EFFECTS OF LIGHT, EPIPHYTES AND GRAZERS

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Contract No. X003246

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CHESAPEAKE BAY PROGRAM
OFFICE OF RESEARCH AND DEVELOPMENT
U.S. ENVIRONMENTAL PROTECTION AGENCY
ANNAPOLIS, MD 21401

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NATIONAL TECHNICAL
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SPRINGFIELD, VA. 22161

TECHNICAL REPORT DATA

(Please read Instructions on the reverse before completing)

1. REPORT NO. EPA-600/3-83-019

2.

3. RECIPIENT'S ACCESSION NO. PB83 189365

4. TITLE AND SUBTITLE
Submerged Aquatic Vegetation: Distribution and Abundance in the Lower Chesapeake Bay and the Interactive Effects of Light, Epiphytes, and Grazers

5. REPORT DATE April 1983

6. PERFORMING ORGANIZATION CODE VIMS

7. AUTHOR(S)
Orth, Moore, and Montfrans

8. PERFORMING ORGANIZATION REPORT NO.

9. PERFORMING ORGANIZATION NAME AND ADDRESS
Virginia Institute of Marine Science
Gloucester Point, Virginia 23062

10. PROGRAM ELEMENT NO. B44B2A

11. CONTRACT/GRANT NO. X - 003246

12. SPONSORING AGENCY NAME AND ADDRESS
U.S. EPA - Chesapeake Bay Program
2083 West Street, Suite 5G
Annapolis, Maryland 21401

13. TYPE OF REPORT AND PERIOD COVERED

14. SPONSORING AGENCY CODE EPA/600/05

15. SUPPLEMENTARY NOTES

16. ABSTRACT

This final grant report is subdivided into two major sections. the first section describes the distribution and abundance of submerged aquatic vegetation (SAV) in the lower Bay. Baseline information for SAV was collected in 1978 and supplemented with additional information from 1979. Subsequently, in 1980 and 1981, overflights were conducted of all polyhaline and mesohaline areas mapped for SAV in 1978 and photographs were taken from which aerial coverage of the vegetation was measured. The data from 1978 through 1981 were analyzed for short term changes in SAV distribution and abundance. This information was combined with historical data from six intensive study sites to provide a detailed description of changes in distribution and abundance of SAV over the last 50 years.

17. KEY WORDS AND DOCUMENT ANALYSIS

a. DESCRIPTORS	b. IDENTIFIERS/OPEN ENDED TERMS	c. COSATI Field/Group

18. DISTRIBUTION STATEMENT
Unrestricted distribution

19. SECURITY CLASS (This Report) unclassified

20. SECURITY CLASS (This page) unclassified

21. NO. OF PAGES 143

22. PRICE

EPA Form 2220-1 (9-73)

NOTICE

This document has been reviewed in accordance with U.S. Environmental Protection Agency policy and approved for publication. Mention of trade names or commercial products does not constitute endorsement or recommendation for use.

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ACKNOWLEDGMENTS

We would like to thank the following people for their indispensable help in the completion of this project: Charlie Alston who aided in the flight organization and aerial photography; Sam White who piloted the VIMS aircraft; Anna Vascott, Linda Lee, Jamie Topping and Glenn Markwith for their valuable assistance in the tedious work made necessary in the grazing experiments; Cliff Ryer, who in addition to aiding in laboratory experiments, provided expert assistance in the data analysis; Judy Capelli, who was indispensible in all aspects and provided more than just technical assistance; Shirley Sterling, Carole Knox, Nancy White and the VIMS art, photographic and report center for the preparation of this report. Finally, to all those individuals who have played a role in the Chesapeake Bay Program and making it possible for all the exciting research on submerged aquatic vegetation to continue, we are forever indebted.

PREFACE

This final grant report is subdivided into two major sections. the first section describes the distribution and abundance of submerged aquatic vegetation (SAV) in the lower Bay. Baseline information for SAV was collected in 1978 and supplemented with additional information from 1979. Subsequently, in 1980 and 1981, overflights were conducted of all polyhaline and mesohaline areas mapped for SAV in 1978 and photographs were taken from which aerial coverage of the vegetation was measured. The data from 1978 through 1981 were analyzed for short term changes in SAV distribution and abundance. This information was combined with historical data from six intensive study sites to provide a detailed description of changes in distribution and abundance of SAV over the last 50 years.

Included in this section of the report are: 1) a comparison of SAV distribution and abundance for all topographic quadrangles containing SAV in 1978, 1980 and 1981; 2) a complete analysis of information from six historical sites including the most recent 1980 and 1981 data; and 3) an appendix which includes the topographic maps with SAV bed outlines for the 1980 inventory. These are directly comparable to maps produced from photography taken in 1978.

A separate report entitled "Distribution and Abundance of SAV in the Chesapeake Bay: A Scientific Summary" was submitted to the Chesapeake Bay Program previously. This report summarizes results from research conducted over the last four years by the Johns Hopkins University, The American University, Earth Satellite Corporation and the Virginia Institute of Marine Science and strives to answer key Bay management questions related to SAV.

Section two deals with the interactive effects of light, epiphytes and grazers on SAV and has been written in three chapters. The first chapter reviews the literature on epiphyte-seagrass relationship with an emphasis on the role of micrograzing. The second chapter examines the salinity tolerances of *Bittium varium* adults and larvae and attempts to relate population changes of this important epifaunal grazer to salinity perturbations caused by Tropical Storm Agnes. The third chapter of this section further studies the role of the gastropod, *Bittium varium*, in an eelgrass community. The results of preliminary laboratory experiments in a previously sponsored EPA Chesapeake Bay Program study, "The Functional Ecology of Eelgrass" (Orth and van Montfrans, 1982) revealed that *B. varium* substantially reduced periphyton on eelgrass blades. The decline of eelgrass along the western shore of the Bay one year following the drastic decline of *B. varium* in the same region during 1972 (Orth, 1977), suggested a causal relationship between the removal of periphyton by this grazing snail and the vigor of eelgrass (*Zostera marina*). We therefore formulated and tested the hypothesis that the presence of *Bittium varium* enhances the growth and vigor of eelgrass by removing epiphytes, which are known to reduce photosynthesis through restricting light and bicarbonate ion uptake (Sand-Jensen, 1977). If the hypothesis is true, the presence of *B. varium* and other grazers could be important for eelgrass distribution, particularly in areas where light reaching the plant surface may be only marginally adequate for photosynthetic maintenance. The results of our experiments are discussed in regard to this concept.

SECTION I

DISTRIBUTION AND ABUNDANCE OF SUBMERGED AQUATIC VEGETATION IN THE LOWER CHESAPEAKE BAY 1978-1981

by

Robert J. Orth
and
Kenneth J. Moore

INTRODUCTION

Submerged aquatic vegetation (SAV) has been the subject of an intensive research program funded by the U.S. Environmental Protection Agency's Chesapeake Bay Program since 1978. One of the main elements of the SAV research was an analysis of the distribution and abundance of SAV. In 1978, a baywide survey of SAV using aerial photography was conducted. The results provided scientists and resource managers the first comprehensive look at the current distribution and abundance of SAV in the Chesapeake Bay (Anderson and Macomber, 1980; Orth et al., 1979). In addition, an historical analysis was made of several key sites in the Bay by archival aerial photography dating to 1937.

Because of interest in the rapid changes that have occurred with SAV in the last 15 years (Orth and Moore, 1981a,b), and the relationship that this Chesapeake Bay Program project had with the other projects funded by EPA for the study of Bay grasses, continued observation was made of most areas with significant abundances of SAV in the lower Bay in 1979. This effort was extended in 1980 and 1981 to include aerial photography of all areas mapped for SAV in 1978. This provided complete coverage of SAV over a four year period for the lower Bay. It also allowed for an intensive examination of changes in the distribution and abundance on a short term basis.

MATERIALS AND METHODS

Mapping of Submerged Aquatic Vegetation

The mapping submerged aquatic vegetation is graphically depicted in Figure 1. The method consists of acquiring photography, transferring the SAV bed outlines to base maps and determining the areas of the SAV beds. Each component of the procedure is more fully described below. These procedures are similar to those used in the distribution and abundance work conducted in 1978 (Orth, Moore and Gordon, 1979).

Aerial photography

The first phase of the aerial photography effort was the planning of flight lines for complete areal coverage of all areas of SAV contained within the designated quadrangles. All 27 quadrangles (1:24,000 scale) mapped in 1978 from the polyhaline and mesohaline areas of the lower Bay were examined in 1980 and 1981. Flight lines were drawn on 1:250,000 scale USGS topographic sheets, 2° by 1° series, using a transparent framesize overlay for coverage at an

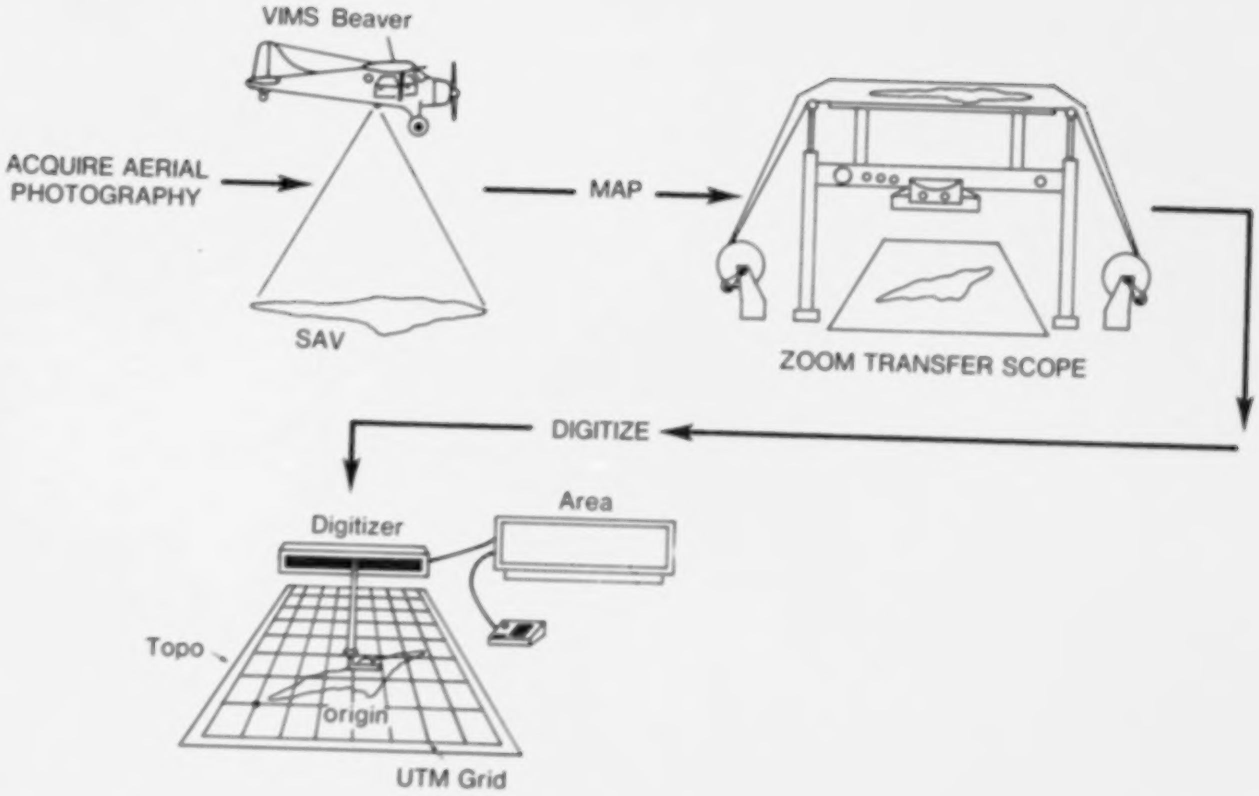

VIMS Beaver
ACQUIRE AERIAL PHOTOGRAPHY
SAV
MAP
ZOOM TRANSFER SCOPE
DIGITIZE
Digitizer
Area
Topo
origin
UTM Grid

Figure 1. Transfer of SAV distribution information from photography to topographic maps.

altitude of 3660 m (12,000 feet). Flight lines were situated to ensure both complete bed coverage and inclusion of land features as control points for mapping accuracy. Lines were also oriented to facilitate ease of flying where possible. Flight direction was oriented such that the overall mission would progress in the same direction as the tide propagation to ensure photography at the lowest possible tidal stage.

The general guidelines used for mission planning and execution were developed in discussions with EPA (Table 1). These quality assurance guidelines address tidal stage, plant growth, sun elevation, water transparency and atmospheric transparency, turbidity, wind, sensor operation, and plotting. Although it was the overall intent to plan for optimum conditions in all items, some constraints are necessarily more important than others and an order of priorities was established to guide mission planning.

The most critical of those items listed is plant growth stage. At the wrong time of year, it would be possible to fly an otherwise ideal mission and record little or no SAV. For the predominant species of grass in the southern Chesapeake Bay, eelgrass, Zostera marina, and widgeon grass, Ruppia maritima, early summer offers the best chance of recording maximum plant coverage. This measurement of maximum standing crop provides the best analysis of that year's productivity at minimum cost.

Flight mission for acquisition of aerial photographs occurred on May 19 and June 5 in 1980 and on June 8 and 28 in 1981. The information on the distribution and abundance of SAV from these two years was compared to the baseline information acquired for the Chesapeake Bay Program in 1978 on June 7, 29 and July 6. Because the aerial photography was taken at approximately the same time period, representing a period when the growth of SAV in the lower Bay would be similar, imagery from all three years should be directly comparable.

Aerial photographs of SAV were also taken in 1979. Because flights were conducted in the fall, when SAV biomass is reduced compared to the early summer period when SAV biomass is high (Orth, et al., 1979), the seasonally biased 1979 information is not used in this report.

The next most important condition affecting the value of the imagery is water transparency. This variable is itself a function of wind, tide, and turbidity (often related to weather during the previous 12 hours). Atmospheric transparency is also important since a high sunlight-to-skylight ratio yields the best SAV-bottom contrast. Sun elevation is also a consideration since at high elevations (sun too high in the sky) sun glint will appear in a portion of the frame, masking the grass or other features used for mapping. This effect is minimized, however, by the proper choice of frame overlap and flight line side lap. Sun elevations were kept between 25° to 45°.

TABLE 1. GUIDELINES FOLLOWED DURING ACQUISITION OF AERIAL PHOTOGRAPHS

1. Tidal Stage - Photography was acquired at low tide, +/- 0-1.5 ft., as predicted by the National Ocean Survey tables.

2. Plant Growth - Imagery was acquired when growth stages ensured maximum delineation of SAV, and when phenologic stage overlap was greatest.

3. Sun Angle - Photography was acquired when surface reflection from sun glint did not cover more than 30 percent of frame. Sun angle was generally between 20° and 40° to minimize water surface glitter. At least 60 percent line overlap and 20 percent side lap was used to minimize image degradation due to sun glint.

4. Turbidity - Photography was acquired when clarity of water ensured complete delineation of grass beds.

5. Wind - Photography was acquired during periods of no or low wind. Off-shore winds were preferred over on-shore winds when wind conditions could not be avoided.

6. Atmospherics - Photography was acquired during periods of no or low haze and/or clouds below aircraft. There was no more than scattered or thin broken clouds, or thin overcast above aircraft, to ensure maximum SAV to bottom contrast.

7. Sensor Operation - Photography was acquired in the vertical with less than 5 degrees tilt. Scale/altitude/film/focal length combination permitted resolution and identification of one square meter area of SAV (surface).

8. Plotting - Each flight line included sufficient identifiable land area to assure accurate plotting of grass beds.

Aircraft scheduling was done in advance around windows in the morning and afternoon (2 to 3 hours) near low tide for specific regions in Chesapeake Bay. NOAA tide tables were used for prediction of tidal stage throughout the Bay, and a table of suggested flight windows was made for a one to two month period. The times from 1100 to 1300 EDT were generally avoided to minimize sun glint problems. The actual decisions to fly on a particular day was made in the early morning, based on forecasts of regional weather systems, previous local weather (24 hours), and most important, current conditions. Because of weather variation, it was generally not possible to pick an "ideal" day for aerial photography in advance.

The camera used for all aerial photography of SAV was a Fairchild CA-8 cartographic camera with a 152 mm (6 1/2-inch) focal length Bausch and Lomb Metrogon lens. Film was Kodak 24 cm (9 1/2-inch) square positive transparency Aerochrome MS, type 2448, loaded into magazines in advance. The camera was mounted in a camera port in the belly of the VIMS single-engine, fixed high wind DeHavilland Beaver aircraft. The aircraft provides a stable platform for vertial aerial photography from 300 to 3700 m altitude (1,000 to 12,000 feet).

The camera was checked for vertical orientation before each exposure, using two-axis leveling. Exposures were timed to insure 60 to 65% forward lap (standard frame spacing), and times were adjusted according to flight line direction in relation to winds aloft. Where adjacent parallel lines were flown, 30% side lap was planned to insure mapable quality contiguous coverage. A Wratten 1A haze filter was used inside the cone of the camera to reduce the degrading effect of atmospheric haze on image quality.

Personnel on the aircraft during a mission included a pilot, navigator, and a camera operator. While in the air, the navigator recorded notes as to atmospheric conditions, flight line number, altitude, heading, frame count, camera setting, and any unusual observations on cassette tape with a portable battery operated recorder. The navigator signaled line start and line stop and watched for the flight line drift (making suggested corrections to the pilot) during photography. The navigator was also experienced in the recognition of SAV areas and modified flight lines or added more lines during the mission to ensure better or more complete coverage.

Following exposure the 38 m rolls were refrigerated immediately until they were processed. No more than two weeks elapsed between exposure and processing. Each roll contained some test exposures to permit selection of optimum transport speed and temperature during processing. At the VIMS Remote Sensing Center, the film was carefully reviewed for quality and adequacy of coverage and entered into the Center's photo-index system. Cassette photo-logs were transcribed to typed hard-copy and checked against the film.

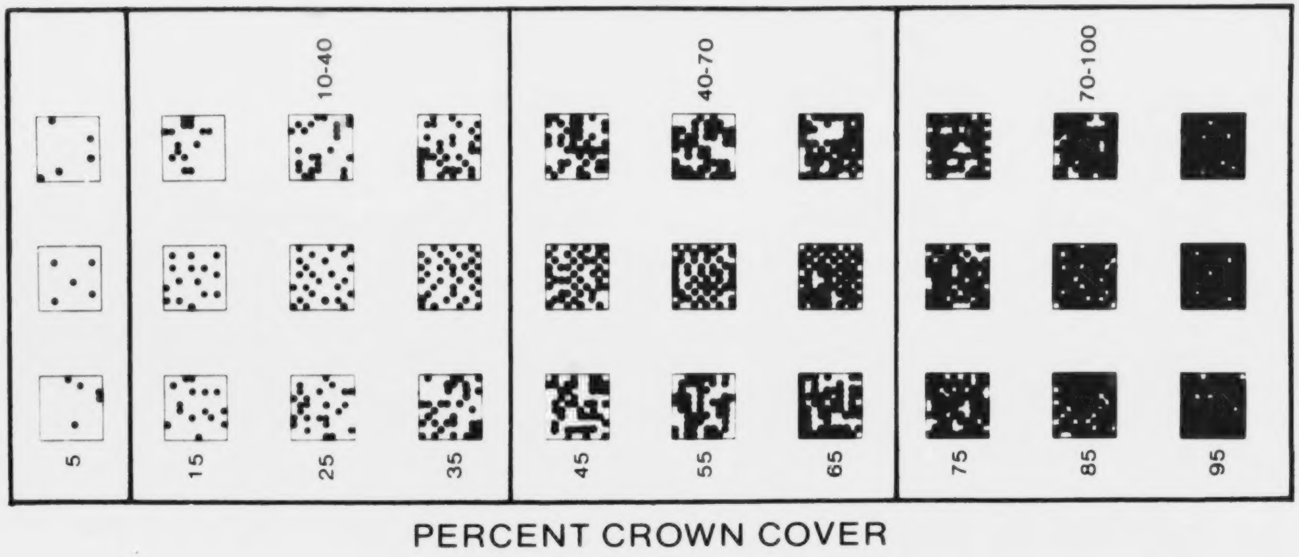
Mapping Process

Before mapping, the film was reviewed by photointerpretor and a biologist to select individual frames for best SAV coverage. The SAV beds were identified using all available information, including knowledge of aquatic grass signatures on the film, areas of grass coverage from previous flight, ground information, and aerial visual surveys. An estimate of percent cover within each seagrass bed was made visually in comparison with an enlarged Crown Density Scale, similar to those developed for estimates of forest tree crown cover from aerial photography (Figure 2). Bed density was classified into one of four categories based on an objective comparison with the density scale. These were: 1. very sparse, (<10%); 2. sparse (10 to 40%); 3. moderate (40 to 70%); or 4. dense (70 to 100%). Either the entire bed, or sub-sections within the bed, were assigned a number (1 to 4) corresponding to the above density categories.

A Bausch and Lomb Zoom Transfer Scope, model ZT-4H, was used to trace the delineated SAV bed boundaries from the aerial photography to base maps of 1:24,000 scale USGS paper topographic (7 1/2-m minute series) quadrangles. The Zoom Transfer Scope enables the operator to view the photograph and the map simultaneously, adjust scale, rotate, and translate one in relation to the other optically, draw the bed outlines and grass density information directly onto the base map. Non-changing features common to the imagery and the topograhic quadrangle, such as road intersections, houses, creeks, etc., were used for alignment and scaling purposes. After transfer of the bed outlines onto the base maps the maps were reviewed with the aerial photography to insure accurate coverage. The original paper topographic quadrangles have been filed at VIMS for future reference. Translucent, mylar stable-base topographic quadrangles were placed over the original base maps, and SAV bed outlines and density information were transferred with black ink for 1980 data only, based on the original grant agreement. Data for the 1981 SAV distribution and abundance which had not been specified in the original grant agreement but was obtained that year was also placed on paper topographic quadrangles. However, bed outlines were not transferred to mylar stable-base quadrangles.

Area Measurement

Areas of SAV beds mapped in both 1980 and 1981 were derived from the 1:24,000 scale topographic quadrangles. Measurements were made on a Numonics Graphics Calculator, model 1224. The unit has a resolution in x and y of 0.24 mm and has registers for scaling and unit conversion so that areas can be read out in any units desired at map scale. Accuracy, determined by repetitive measurements of test areas, is better than 2%. Precision (standard deviation divided by the mean) ranges from approximately 2% at 16 mm^2 (10,000 m^2 at a scale = 1:24,000) to well under 1% at 160 mm^2 (100,000 mm^2) with an overall average of 1.4%.



10-40
40-70
70-100
5
15
25
35
45
55
65
75
85
95
PERCENT CROWN COVER

Figure 2. Crown density scale used to estimate SAV percent cover.

Historical Sites

Orth, et al. (1979) mapped the changes in the distribution and abundance of SAV over the last 40 years at six areas in the lower Bay: Guinea Neck and Mumfort Island in the York River, East River in the Mobjack Bay, Parrott Island in the Rappahannock River, Fleets Bay which is located just north of the mouth of the Rappahannock River and Vaucluse Shores on the bayside of the Eastern Shore of Virginia near Cape Charles. The imagery from 1980 and 1981 allowed us to follow each of these areas for continued alterations in the distribution and abundance of SAV.

RESULTS

The aerial photography and subsequent mapping process in 1980 and 1981 resulted in the delineation of SAV presence or absence in 27 topographic quadrangles along the eastern and western shores of the lower Chesapeake Bay (Fig. 3). These areas in the meso- and polyhaline regions were the principal areas mapped in the baseline survey in 1978 (Orth, et al., 1979) and represent areas dominated by eelgrass (*Zostera marina*) and widgeongrass (*Ruppia maritima*). The total area of SAV as represented on each quadrangle for 1980 and 1981 are presented in Table 2 along with data from 1971, 1974 and 1978 for those quadrangles which were mapped for SAV in those years (Orth and Gordon, 1975; Orth et al., 1979). Discussion of the distribution and abundance of SAV in the lower Bay is presented below based on major sections of the Bay rather than individual topographic quadrangles (e.g. the York River rather than Clay Bank, Achilles, Yorktwon and Poquoson West quadrangles) (Table 3).

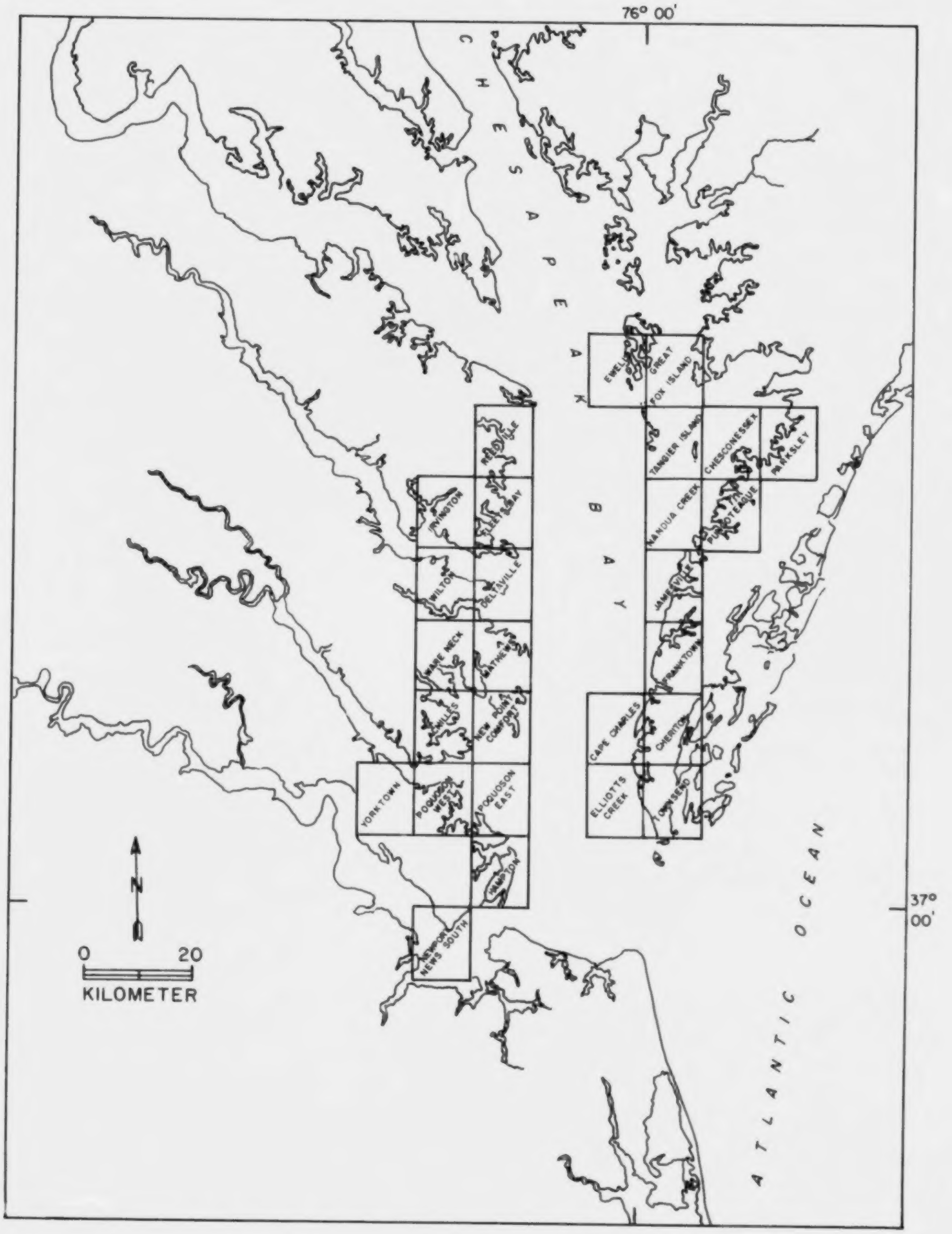
James River Section (includes Newport News South and Hampton Quadrangles)

Very little SAV had been observed in this area in the last 10 years (Tables 2 and 3). Most of the SAV was restricted to very patchy beds distributed along the shoreline from Newport News Point to the Hampton Roads Bridge Tunnel. These few areas that had SAV in 1978 showed no evidence of vegetation in 1980 and or 1981.

Lower Western Shore (includes Hampton, Poquoson East and Poquoson West Quadrangles)

The changes in the distribution and abundance of SAV in the lower Western Shore over the last 10 years (Tables 2 and 3) demonstrates a pattern similar to that found in many other sites around the lower Bay. This is, there was a marked decline observed between 1971 and 1974 followed by relative stability since then, with perhaps a moderate increase in density and expansion of the remaining beds since 1978.

Declines of vegetation between 1971 and 1974 occurred principally in the most upriver, vegetated portions of the Back and Poquoson River, where a complete loss was observed, and in the beds fringing along the Chesapeake Bay where there was decrease in size and density.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C H E S A P E A K E B A Y
EWELL
GREAT FOX ISLAND
TANGIER ISLAND
CHESCONESSEX
PARKSLEY
NANDUA CREEK
PUNGOTEAGUE
JAMESVILLE
FRANKTOWN
CAPE CHARLES
CHERITON
ELLIOTTS CREEK
TOWNSEND
REEDVILLE
IRVINGTON
FLEETS BAY
WILTON
DELTAVILLE
WARE NECK
MATHEWS
ACHILLES
NEW POINT COMFORT
YORKTOWN
POQUOSON WEST
POQUOSON EAST
HAMPTON
NEWPORT NEWS SOUTH
N
0
20
KILOMETER
37° 00'
A T L A N T I C O C E A N

Figure 3. Locations of topographic quadrangles in Virginia which were covered with aerial photography for SAV in 1980.

TABLE 2. TOTAL AREAS OF SAV BY TOPOGRAPHIC QUADRANGLES FOR 1971, 1974, 1978, 1980, 1981

Quadrangle	Area (m^2) by Year				
	1971	1974	1978	1980	1981
Newport News South	--	--	18,700	0	0
Hampton	2,958,100	3,064,600	2,182,500	1,737,666	2,189,321
Poquoson East	9,456,000	4,355,900	5,166,300	6,454,873	5,963,577
Poquoson West	4,892,900*	3,681,700*	2,104,400	1,824,570	1,965,480
Yorktown	*combined with Poquoson West		19,200	0	0
Clay Bank++	1,134,100	120,800	0	0	0
Achilles++	7,450,900	7,417,200	7,979,800	5,637,557	5,474,717
New Point Comfort++	7,254,200	9,662,600	10,963,100	9,203,702	8,585,267
Ware Neck	1,535,600	1,890,000	2,560,000	1,209,480	1,705,972
Mathews	3,401,100	608,900	638,800	308,970	357,840
Wilton++	2,960,700	79,000	104,300	0	0
Deltaville	5,432,900	230,000	594,300	3,839	0
Irvington	1,133,300	0	53,100	0	0
Fleets Bay++	--	1,975,600	1,332,300	181,290	966,048
Reedville	--	--	2,304,000	135,096	363,276
Elliotts Creek	--	--	445,800	81,314	--
Townsend	--	--	427,000	--	--
Cape Charles	--	--	3,214,200	2,049,636	2,526,171
Cheriton	--	--	852,000	522,366	432,108
Franktown++	--	--	5,044,900	3,546,046	3,254,328
Jamesville	--	--	4,060,400	2,416,614	2,778,054
Nandua Creek	--	--	1,848,600	1,688,202	2,633,837
Pungoteague	--	--	4,016,300	3,395,910	5,207,191
Tangier Island	--	--	4,050,600	2,388,977	3,747,357
Chesconessex	--	--	4,825,400	5,264,364	5,969,148
Parksley	--	--	803,500	580,806	1,437,648
Ewell	--	--	14,479,000	13,509,303	13,823,482
Great Fox Island	--	--	3,979,000	2,459,814	3,040,386

Note: -- indicates that aerial photography for SAV within Quadrangle was not available.

++ Quadrangles that contained historically mapped areas.

TABLE 3. NUMBERS OF HECTARES OF BOTTOM COVERED WITH SUBMERGED AQUATIC VEGETATION IN 1971, 1974, 1978, 1980, and 1981 FOR DIFFERENT SECTIONS IN THE LOWER BAY ZONE (NUMBERS OF HECTARES ROUNDED OFF TO NEAREST WHOLE NUMBER) (* INDICATES SECTIONS THAT WERE NOT MAPPED THAT YEAR) (DATA FROM ORTH AND GORDON 1975; ORTH et al. 1979; AND UNPUBLISHED DATA)

Section	Year 1971	 1974	 1978	 1980	 1981
Tangier Island Complex (Includes from MD-VA border to Chesconessex Creek)	*	*	2814	2420	2794
Lower Eastern Shore (Chesconessex Creek to Elliotts Creek)	*	*	1991	1370	1691
Reedville (Includes area from Windmill Pt. to Smith Pt.)	*	*	364	31	133
Rappahannock River (Includes Rappahannock and Piankatank Rivers, and Milford Haven)	1273	68	93	3	43
New Point Comfort Region	168	233	271	182	207
Mobjack Bay (Includes East, North, Ware, and Severn Rivers)	1294	1593	1785	1317	1275
York River (Clay Bank to mouth of York)	493	141	157	135	142
Lower Western Shore (Includes Poquoson and Back Rivers)	1620	1069	925	1002	996
James River (Hampton Roads area only)	*	7	9	0	0
TOTAL FOR LOWER BAY ZONE			8409	6460	7281

The photographic evidence indicates that although the vegetation in this region has not increased significantly in area since 1978, the beds have become somewhat more dense. However, there is little evidence of regrowth to the former upriver limits of the distribution.

York River (includes Poquoson West, Yorktown, Clay Bank and Achilles Quadrangles)

Between 1971 and 1974 significant declines of vegetation in the York River section (Tables 2 and 3) occurred principally in the most upriver beds. Most of these denuded areas were found in the region bounded by the Clay Bank and Yorktown quadrangles (Table 2). By 1974 only scattered small patches of vegetation remained of the formerly extensive beds of eelgrass and widgeon grass at these upriver sites. By 1978, these too had largely disappeared.

Those beds of vegetation found closer to the mouth of the river in 1971 (portions of the Achilles and Poquoson West quadrangles) also declined significantly between 1971 and 1974. However, as proximity to the mouth of the River increased, the dieback was less extensive, such that there was an increase in the percentage of each bed remaining. This partial reduction compares to the almost complete decline experienced 5 to 10 km upriver during the same period. The pattern of decline evident in these lower York River beds was one of loss of vegetation in the deeper offshore sections of the beds with survival of vegetation in the nearshore zone. However, these differences in depth where the vegetation remained and where it disappeared represent vertical distances of less than one meter. In most cases the formerly vegetated areas consist of wide, shallow flats 100 m to 1000 m wide with little or only moderate slopes and depths ranging from 0 to 1 meter below MLW.

Evidence indicates that the decline of SAV in the York River occurred quite rapidly. Although comprehensive aerial photography of the region is available only for the years 1971 and 1974, archival search of photographic records revealed several other overflights during the 1971-1974 period. They document the persistence of dense beds of SAV as late as April 1973 in areas showing significant losses by the summer of 1974. This would suggest that much of the loss occurred within one year, between the summer of 1973 and the summer of 1974. Since recent studies of SAV biology and transplantation in the Chesapeake Bay have revealed that the remaining vegetation in this region undergoes significant annual late-summer diebacks, we feel it is very possible that an extreme dieoff during July and August of 1973 related to high temperatures, low light levels and the absence of the periphyton grazers may have been responsible for the lack of vegetation in 1974.

There is no evidence as yet to suggest the decline of the vegetation occurred in one area of the river before another. In fact, it appears that the decline of the vegetation occurred simultaneously in all the areas but that the severity of the decline varied from site to site.

From 1978 to 1980 the vegetation in the York had remained relatively stable in aerial distribution. Since 1980 however we have observed some regrowth by seedlings onto denuded sand flats in the vicinity of remnant SAV beds in the lower York. During the spring of 1982 we observed that many of the seedlings evident in 1980 and 1981 had grown into small patches (1 m^2) of vegetation. There has been as yet no regrowth into the completely denuded upriver sites. Eelgrass transplanted into these upriver areas during 1980 and 1981 died during the July-August period while those transplanted in areas where the seedlings occur have survived (Orth and Moore, 1982).

SAV at two of the historical sites in the York River chosen for intensive mapping, declined between 1971 and 1974 (Table 4, Fig. 4). SAV at the Mumfort Island site was completely gone by 1978 while at the Jenkins Neck site, some vegetation persisted through 1978 and now has increased through 1981. Much of this increase, as mentioned above, appears to be a result of successful recruitment from seeds and their subsequent rapid growth. This new growth is occurring in the most shallow areas close to land while little or no revegetation is occurring in the offshore, deeper areas, except for some replanted areas adjacent Allens Island (Orth and Moore, 1982).

Mobjack Bay and New Point Comfort (includes Achilles, New Point Comfort, Ware Neck and Mathews Quadrangles)

The Mobjack Bay and its adjacent New Point Comfort section of the lower Chesapeake Bay have been characterized by a less severe decline SAV beds over the last 10 years compared to areas such as the York and Rappahannock rivers (Tables 2 and 3). Where declines have occurred since 1971 they have primarily been in the offshore, deeper sections of the broad beds fringing the Mobjack Bay and in the upstream sections of its associated rivers (Severn, East).

The historically mapped site at the mouth of the East River (Table 4, Fig. 4) typifies the pattern of the offshore to inshore loss of SAV. A detailed overlay of this site from 1974 to 1981 shows the alteration of the SAV bed primarily along the outer fringe (Fig. 5).

This pattern of limited declines since 1971 in the areas fringing along the bays and more severe changes in the tributaries follows that of most of the other sections around the Virginia portion of the Chesapeake (Orth and Moore, 1981b). This would seem to imply that those factors limiting SAV growth were related to the salinity regime. In those areas where runoff was greatest, thereby reducing salinity, turbid water conditions also were associated representing additional stress on the plants.

TABLE 4. AREAS OF SAV AT HISTORICAL MAPPING SITES (LOWER BAY SECTION) 1937-1981

Parrott Islands

Date	<10%	10-40%	Area m^2 40-70%	70-100%	Total
1937	0	297,024	1,598,268	0	1,895,292
1951	394,797	778,146	1,222,410	1,158,384	3,553,737
1960	411,306	631,566	547,014	1,947,372	3,537,258
1968	92,064	1,354,110	1,205,628	124,374	2,776,176
1974	0	2,922	7,710	0	10,632
1978	0	22,872	0	0	22,872
1980	0	0	0	0	0
1981	0	0	0	0	0

Fleets Bay

Date	<10%	10-40%	Area m^2 40-70%	70-100%	Total
1937	0	1,385,424	548,076	744,864	2,678,364
1953	1,488,258	597,354	591,018	284,232	2,960,862
1961	1,572,612	1,330,140	1,643,892	884,280	5,430,924
1969	1,436,403	1,938,660	1,592,170	270,372	5,237,605
1974	105,714	1,624,884	1,325,040	0	3,055,638
1978	167,688	528,918	33,592	0	730,198
1980	0	121,890	26,040	2,472	150,402
1981	0	683,250	9,816	13,986	707,052

Mumfort Islands

Date	<10%	10-40%	Area m^2 40-70%	70-100%	Total
1937	0	495,060	397,368	23,832	916,260
1953	151,728	699,252	106,356	1,461,846	2,419,182
1960	0	258,210	1,880,238	0	2,138,448
1971	0	685,536	1,088,976	0	1,774,512
1974	0	127,488	23,826	0	151,314
1978	0	0	0	0	0
1980	0	0	0	0	0
1981	0	0	0	0	0

TABLE 4. (continued)

Jenkins Neck

			Area m^2		
Date	<10%	10-40%	40-70%	70-100%	Total
1937	0	1,180,200	820,612	32,520	2,033,332
1953	426,480	647,112	717,180	1,811,832	3,602,604
1960	140,448	794,178	639,012	2,067,948	3,641,586
1971	0	278,586	2,350,380	33,792	2,662,758
1974	93,972	303,804	1,599,228	93,912	2,090,916
1978	132,714	299,760	671,616	162,408	1,266,498
1980	60,810	191,605	690,968	179,589	1,122,972
1981	0	0	763,194	309,012	1,072,206

East River

			Area m^2		
Date	<10%	10-40%	40-70%	70-100%	Total
1937	1,024,010	809,770	1,357,790	85,530	3,277,100
1953	591,840	1,158,490	1,394,740	1,742,050	4,887,120
1963	31,032	1,916,530	2,340,480	0	4,288,042
1971	0	2,007,460	2,253,080	96,620	4,307,160
1974	509,730	348,820	1,955,130	0	2,813,680
1978	47,860	515,000	1,864,850	0	2,427,710
1980	191,520	451,351	808,842	158,634	1,610,347
1981	0	96,174	1,183,542	198,474	1,478,190

Vaucluse Shores

			Area m^2		
Date	<10%	10-40%	40-70%	70-100%	Total
1938	0	1,120,284	1,451,392	1,480,128	4,051,804
1948	506,706	1,171,884	1,715,556	0	3,994,146
1955	1m938,258	0	528,996	1,238,124	3,705,378
1966	452,940	402,324	2,534,178	604,176	3,993,618
1972	286,554	364,764	2,515,740	391,770	3,558,828
1978	187,728	507,054	80,872	2,036,526	2,812,180
1980	359,551	7,098	5,016	1,783,938	2,845,603
1981	327,786	97,950	355,344	1,852,392	2,633,472

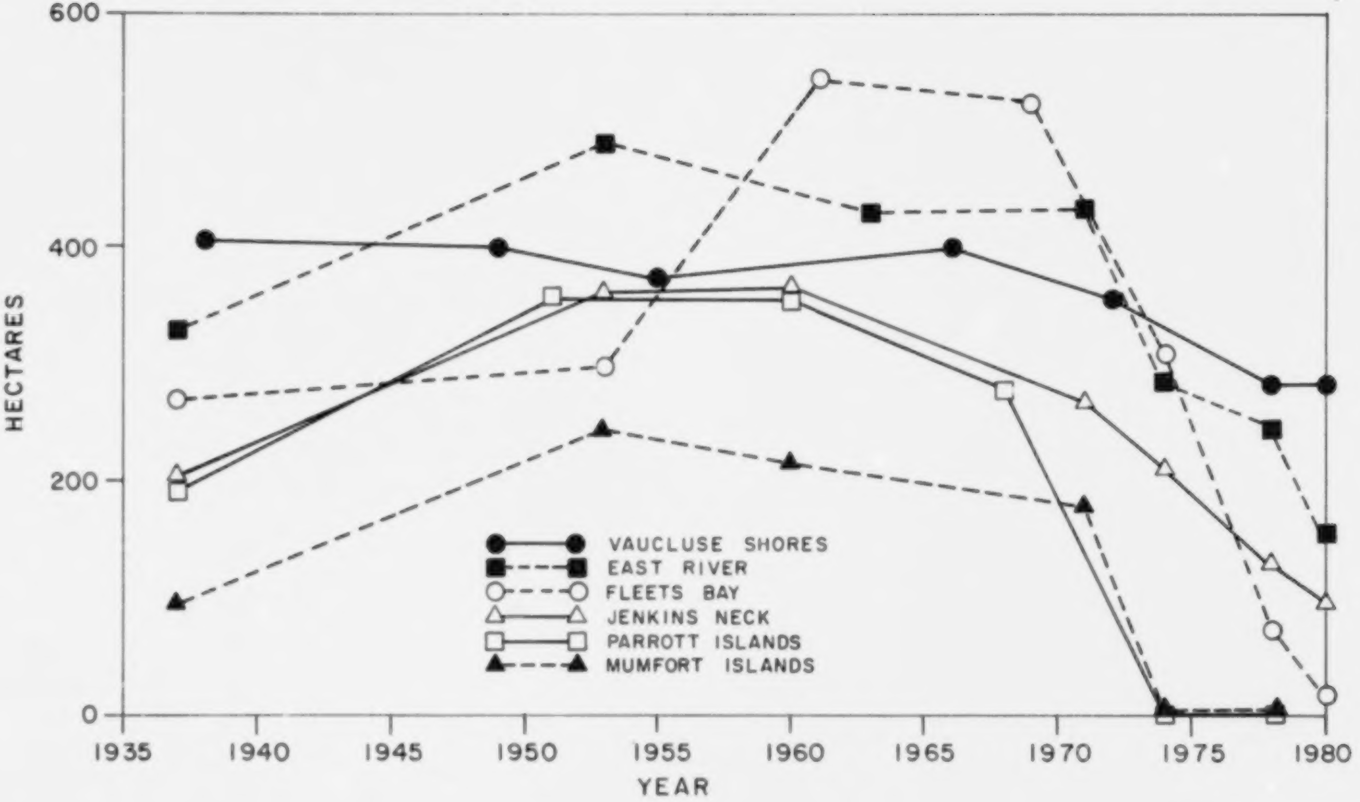

Figure 4. Trends in SAV coverage at six sites in the lower Chesapeake Bay.

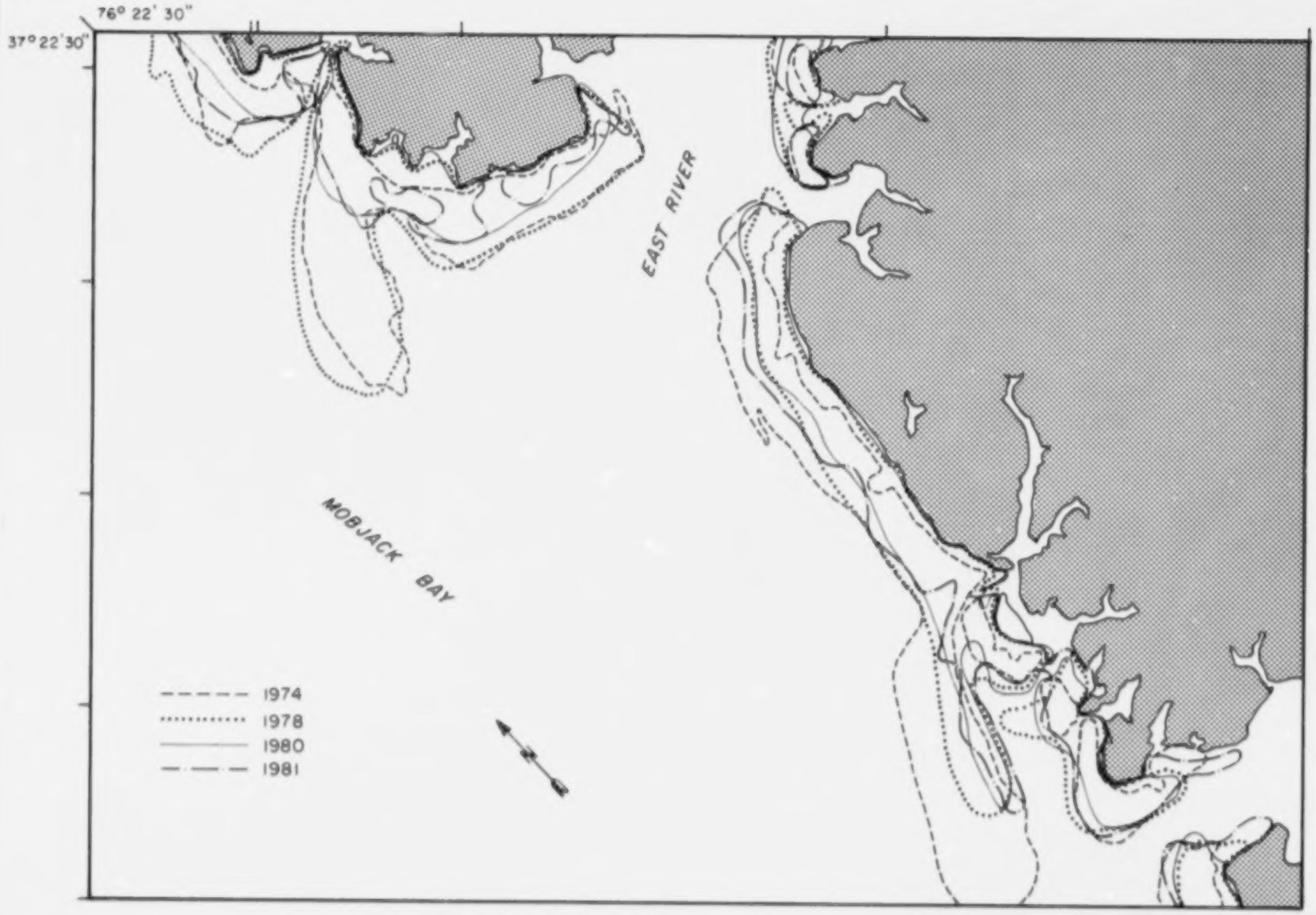
76° 22' 30"
37° 22' 30"
EAST RIVER
MOBJACK BAY
N
1974
1978
1980
1981

Figure 5. Map of mouth of East River and a portion of Mobjack Bay showing changes in SAV distribution from 1974 to 1981.

Rappahannock River Section (includes Mathews, Wilton, Deltaville and Irvington Quadrangles)

Like the York River, the lower Rappahannock River and the adjacent areas of the Piankatank River and Milford Haven in the south experienced a precipitous decline in SAV between 1971 and 1974 (Tables 2 and 3). Formerly extensive beds of eelgrass and widgeon grass, 100 m to 500 m wide, found along most of the shoreline in this section appeared as only scattered patches of vegetation in 1974. Between 1974 and the present, several sparse patches of vegetation have persisted but the abundance of SAV in this particular region may be at the lowest level ever recorded. There has been as yet no evidence of any significant regrowth of SAV in the entire region.

All the SAV at the Parrott Island historical site was gone by 1978 (Orth, et al., 1979) with no regrowth of any SAV between 1978 and 1981 (Table 4, Fig. 4).

Reedville (includes Fleets Bay and Reedville Quadrangles)

Although the aerial photography record is less complete for this section of the lower Bay, extensive beds of SAV are evidenced throughout much of the shoreline until 1974 (Table 2 and 3). By 1978, only relatively sparse areas of SAV represented the remnants of the formerly dense beds of eelgrass and widgeon grass. Between 1978 and 1980 significantly fewer of even these sparse areas were observed, suggesting a gradual loss of the remaining grasses. Some increase in density and area of the remaining beds was observed in 1981 but no widespread recovery was evident.

The Fleets Bay historical site (Orth, et al., 1979) represent the changes that have occurred in this section (Table 4, Fig. 4). The changes at this site differ in one major aspect from the other intensively mapped sites where SAV has declined. The decline in the York River and Parrott Island historical sites occurred between 1971 and 1974. Although 1971 data are lacking for the Fleets Bay site, SAV appeared to undergo a major decline between 1974 and 1980 with a slight increase in area in 1981.

Eastern Shore (includes Elliotts Creek, Townsend, Cape Charles, Cheriton, Franktown, Jamesville, Nandua Creek, Pungoteague, Tangier Island, Chesconessex, Parksley, Ewell and Great Fox Island Quadrangles)

Although quantitative mapping of the entire Eastern shore of the Bay was not done prior to 1978, qualitative analysis of available information as well as the mapping of one historical site at Vaucluse Shores (Table 4) suggest that many of the SAV beds found along this section have not changed appreciably since 1970. Quantitative data since 1978 reveal little significant change over the last few years, especially in the extensive beds in the vicinity of Tangier Island and Smith Islands where much of the vegetation is located (Tables 2 and

3). Some of the variability observed in the vegetation of the more northern topographic quadrangles in this section (i.e. Great Fox Island) may be due to the abundance of widgeongrass associated with the eelgrass. This species reaches a maximun standing crop slightly later in the summer than eelgrass and its coverage as viewed from the air in June appears more variable from year to year than eelgrass. Additional variation is due to the extensive areas of relatively sparse vegetation (<10% cover) found from Nassawadox Creek north. The observable bed outlines of many of these areas of viewed from the air may vary considerably from year to year. If converted to biomass however, the impact of these changes in aerial coverage would be greatly reduced.

Many of the SAV beds found along this Eastern shore section are protected by offshore sandbars from the dominant northwest winds. As the sandbars migrate, portions of the existing beds become covered with sand (Orth, et al., 1979). Presumably, as other bar migration forms suitably protected habitat, new SAV beds are formed. The Vaucluse Shore historical site (Fig. 4) is indicative of this phenomenon. We feel that without the protection afforded by these sandbars, SAV would not persist along much of this shoreline (Orth, et al., 1979).

SUMMARY

Beds of submerged aquatic vegetation in the lower Chesapeake Bay were mapped from aerial photography obtained in 1980 and 1981 onto U.S.G.S. topographic quadrangles (1:24,000 scale). Aerial photography was acquired using similar techniques and film and under constraints observed in the acquisition of the 1978 photography to insure maximum delineation of the SAV beds and to obtain comparable data. Only those topographic quadrangles in the polyhaline and mesohaline areas of the lower Bay were monitored in 1980 and 1981, resulting in the mapping of 27 quadrangles. The dominant vegetation consisted of eelgrass and widgeongrass.

In 1980 and 1981, 6460 hectares and 7281 hectares of SAV were mapped, respectively. This compared to 8409 hectares for a similar area in 1978. Reductions of SAV from 1978 to 1980 occurred in all sections of the lower Bay except in the lower western shoreline. Almost no vegetation was found in the Rappahannock River section in 1980 with only a slight increase in 1981. The SAV in the James River in 1978, which existed in a narrow band between Fort Eustis and Newport News Point, was completely absent by 1980.

The predominant SAV beds in 1980 and 1981, were still found in those major areas identified in 1978: 1. along the western shore of the lower Bay between Back River and York River; 2. along the shoreline of the Mobjack Bay and immediately adjacent to the Guinea Marshes at the mouth of the York River; 3. the shoal area between Tangier and Smith Island (this represented the largest and most extensive SAV bed in the entire Bay); 4. behind large protective sandbars near Hungar's Creek and Cherrystone Creek along the Bay's eastern shoreline.

Comparison of the 1980 and 1981 data at the six historical SAV sites mapped in 1978 showed no recovery of any SAV at the Parrott Island (Rappahannock River) and Mumfort Island (York River) site. These two sites remained devoid of any SAV. SAV at the Fleets Bay site continued to decline from 1978 ato 1980 but showed a slight rebound in 1981. At Vaucluse Shores, SAV beds remained relatively stable during this time period. SAV at the East River (Mobjack Bay) site, declined both in 1980 and 1981 from 1978 levels. A comparison of SAV bed formations from 1974 through 1981 (four complete surveys) showed the decline of SAV to have occurred primarily in the deeper, offshore areas rather than the inshore, more shallow locations. This pattern was repeated in many other locations in the lower Bay region. Although total SAV area showed a slight decline in 1980 and 1981 at the Jenkins Neck (York River) site, recruitment by eelgrass seedlings was observed in the vicinity of Allens Island both years and primarily in the more inshore, shallower areas. These seedling grew vigorously and resulted in numerous patches measuring up to one m^2. This pattern was also observed along the York River shoreline from Allens Island to Sarah's Creek.

Since 1978 then, although there has been some overall decrease in the area vegetated with SAV in the lower section of the Bay, the declines we noted between 1978 and 1981 were not as great as the declines that occurred between 1971 and 1978. Indeed, SAV in some areas, for example in the lower York River, have actually increased in abundance between 1980 and 1981. Aerial photography obtained in 1982 (but not mapped) indicate that this trend of increasing SAV abundance continued into 1982. Continued annual mapping will allow us to better define these rapid changes. We therefore strongly recommend an annual monitoring program for SAV using aerial photography. In addition because of the rapid, large scale changes in SAV distribution which can occur within one growing season the shorter the interval between the data the better.

The low cost, efficiency and accuracy of using aerial photography for mapping SAV distribution and abundance are the main advantage of this technique compared to ground surveys. Because of the importance of SAV in the Bay, an annual inventory of this resource should be considered a high priority by state management agencies.

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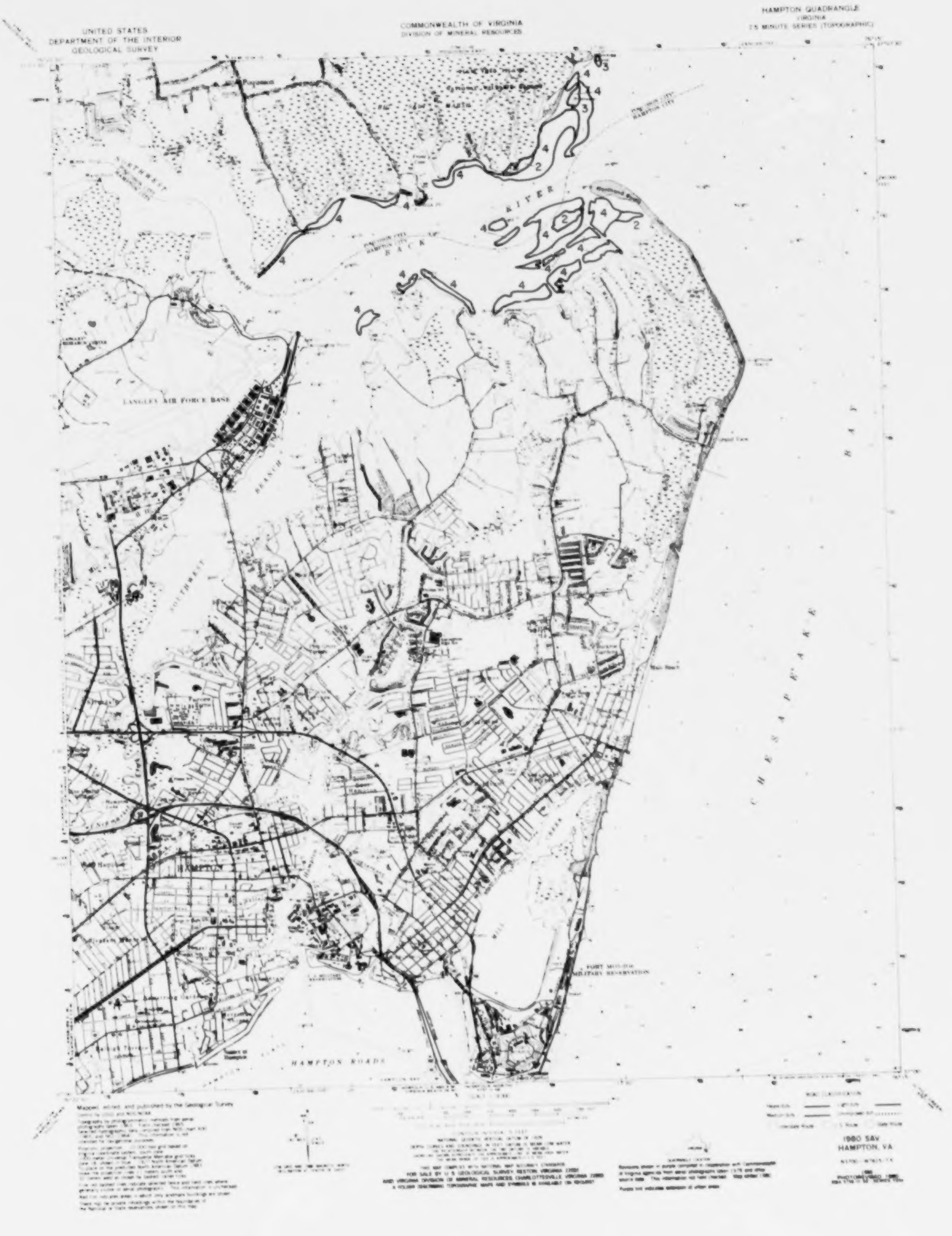
APPENDIX A

TOPOGRAPHIC QUADRANGLES SHOWING THE DISTRIBUTION AND ABUNDANCE OF SAV WHERE SAV WAS PRESENT (1 = <10%; 2 = 10-40%; 3 = 40-70%; 4 = 70-100%).

QUADRANGLES FOR 1981 ARE NOT PRESENTED AS THIS WAS NOT PART OF THE GRANT OBLIGATIONS. PLEASE REFER TO ORTH, MOORE AND GORDON (1979) FOR COMPARISON OF THE 1978 TOPOGRAPHIC QUADRANGLES.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DEPARTMENT OF THE INTERIOR
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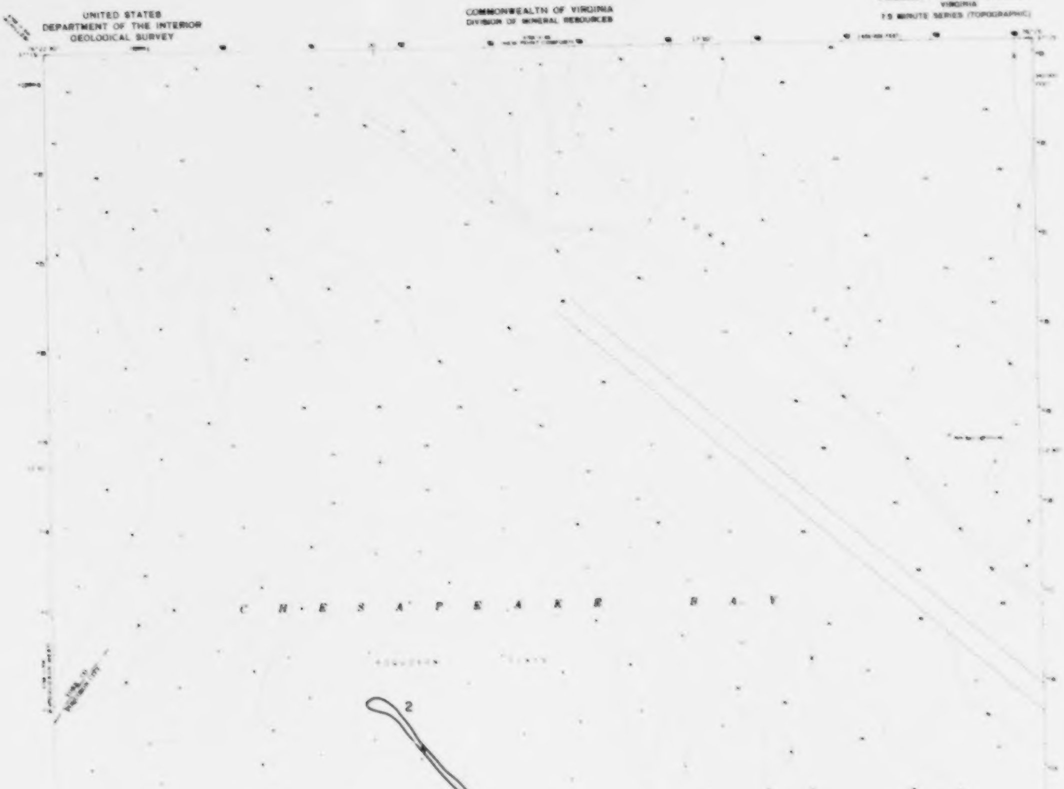
COMMONWEALTH OF VIRGINIA
DIVISION OF MINERAL RESOURCES
HAMPTON QUADRANGLE
VIRGINIA
7.5 MINUTE SERIES (TOPOGRAPHIC)
BACK RIVER
LANGLEY AIR FORCE BASE
SOUTHWEST BRANCH
HAMPTON
CHESAPEAKE BAY
FORT MONROE MILITARY RESERVATION
HAMPTON ROADS
1
2
3
4
ROAD CLASSIFICATION
1980 SAV
HAMPTON, VA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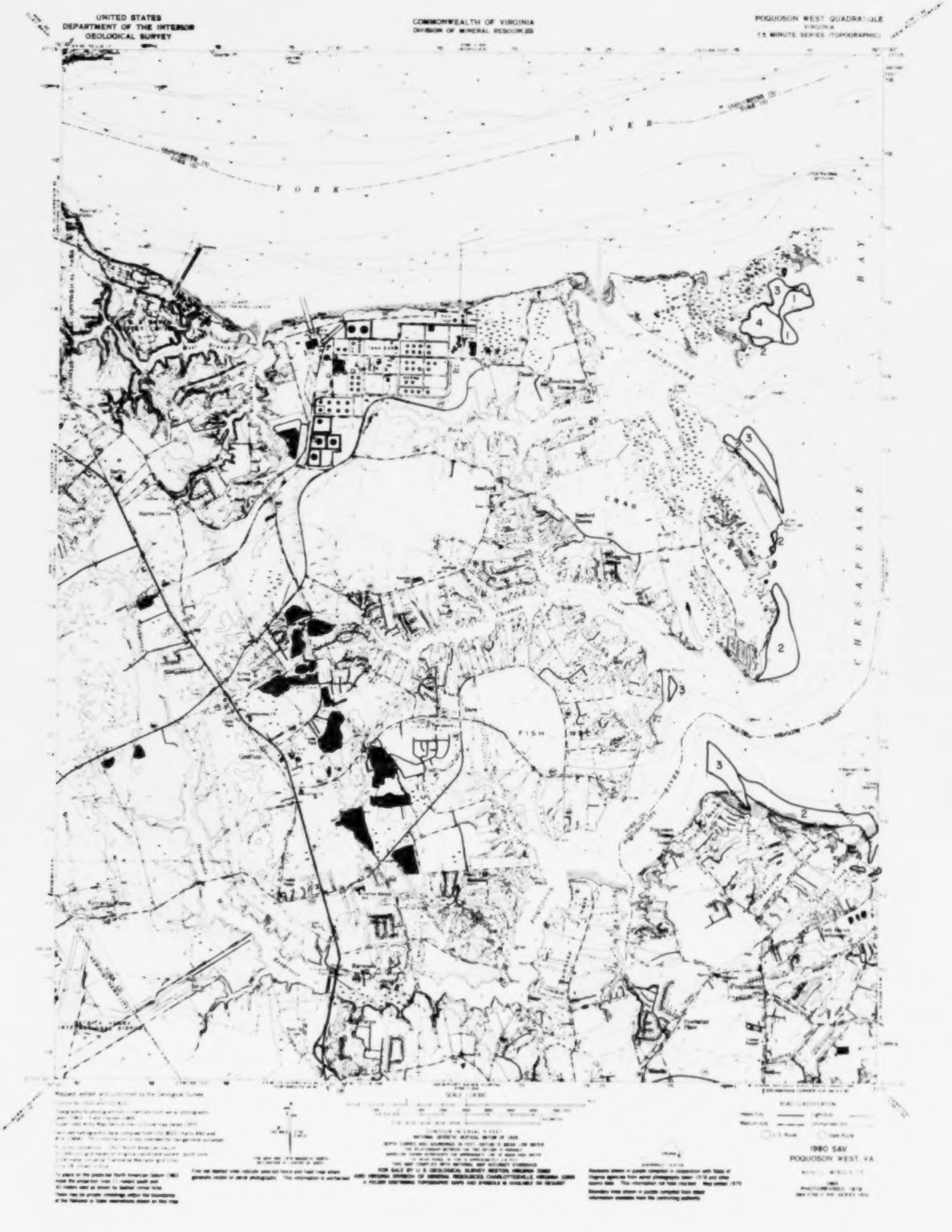
DIVISION OF MINERAL RESOURCES
POQUOSON EAST QUADRANGLE
VIRGINIA
7.5 MINUTE SERIES (TOPOGRAPHIC)
C H E S A P E A K E B A Y
2
3
4
SCALE 1:24 000
CONTOUR INTERVAL 5 FEET
ROAD CLASSIFICATION
1980 SAV
POQUOSON EAST, VA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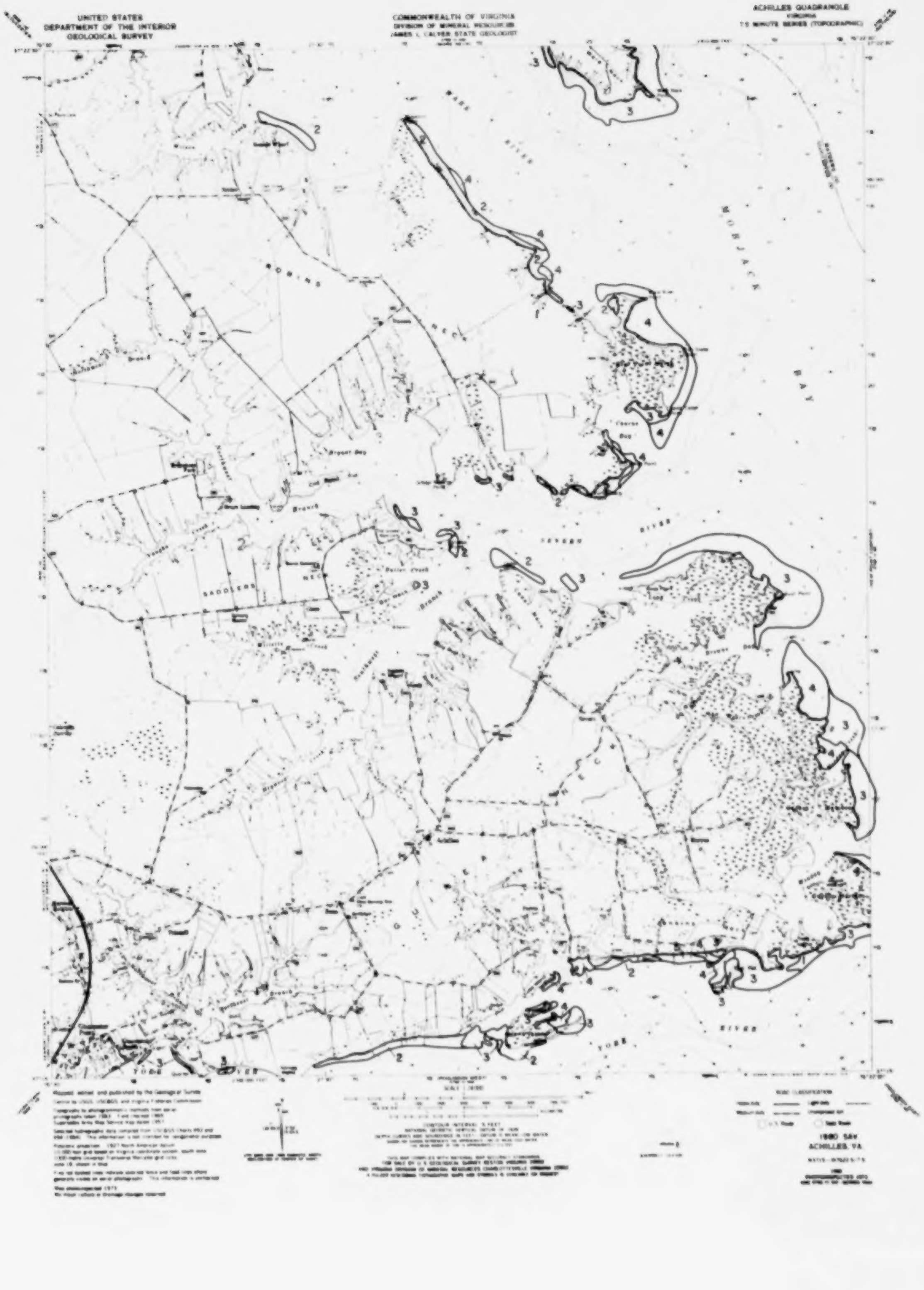
VIRGINIA
7.5 MINUTE SERIES (TOPOGRAPHIC)
YORK RIVER
CHESAPEAKE BAY
FISH
1
2
3
4
SCALE 1:24 000
ROAD CLASSIFICATION
1980 SAV
POQUOSON WEST, VA
PHOTOREVISED 1978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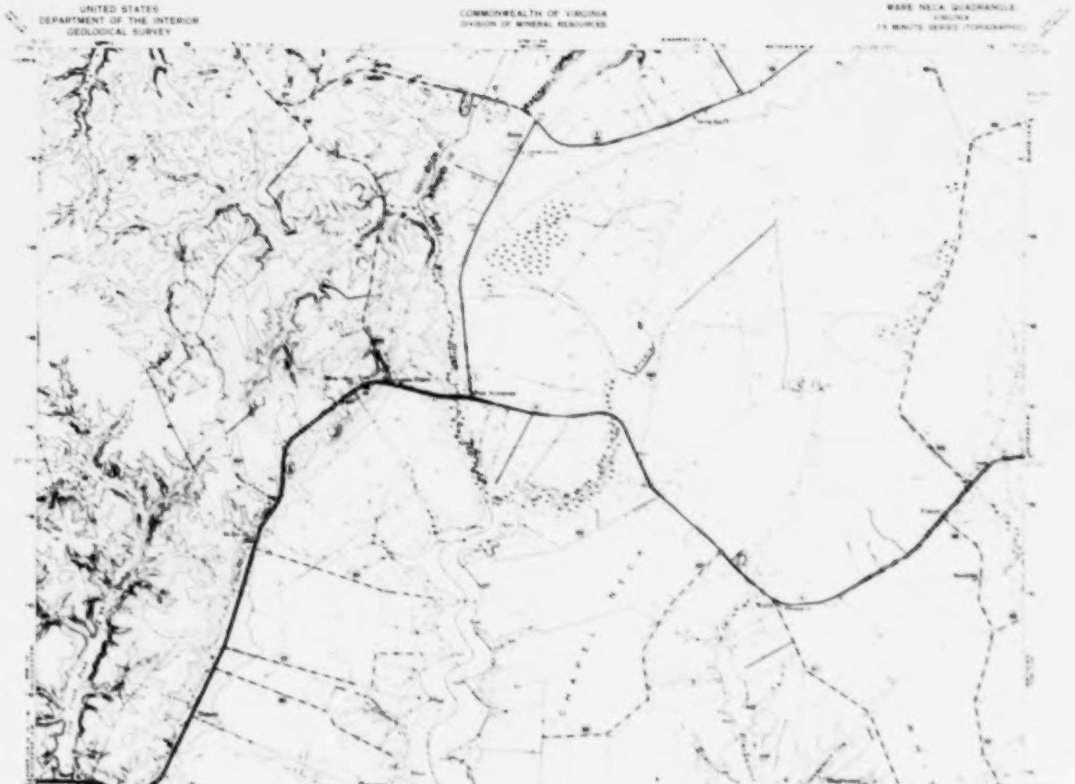
ACHILLES QUADRANGLE
VIRGINIA
7.5 MINUTE SERIES (TOPOGRAPHIC)
MOBJACK
BAY
SEVERN
RIVER
YORK
RIVER
2
3
4
ROAD CLASSIFICATION
1980 SAV
ACHILLES, VA.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VIRGINIA
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2
3
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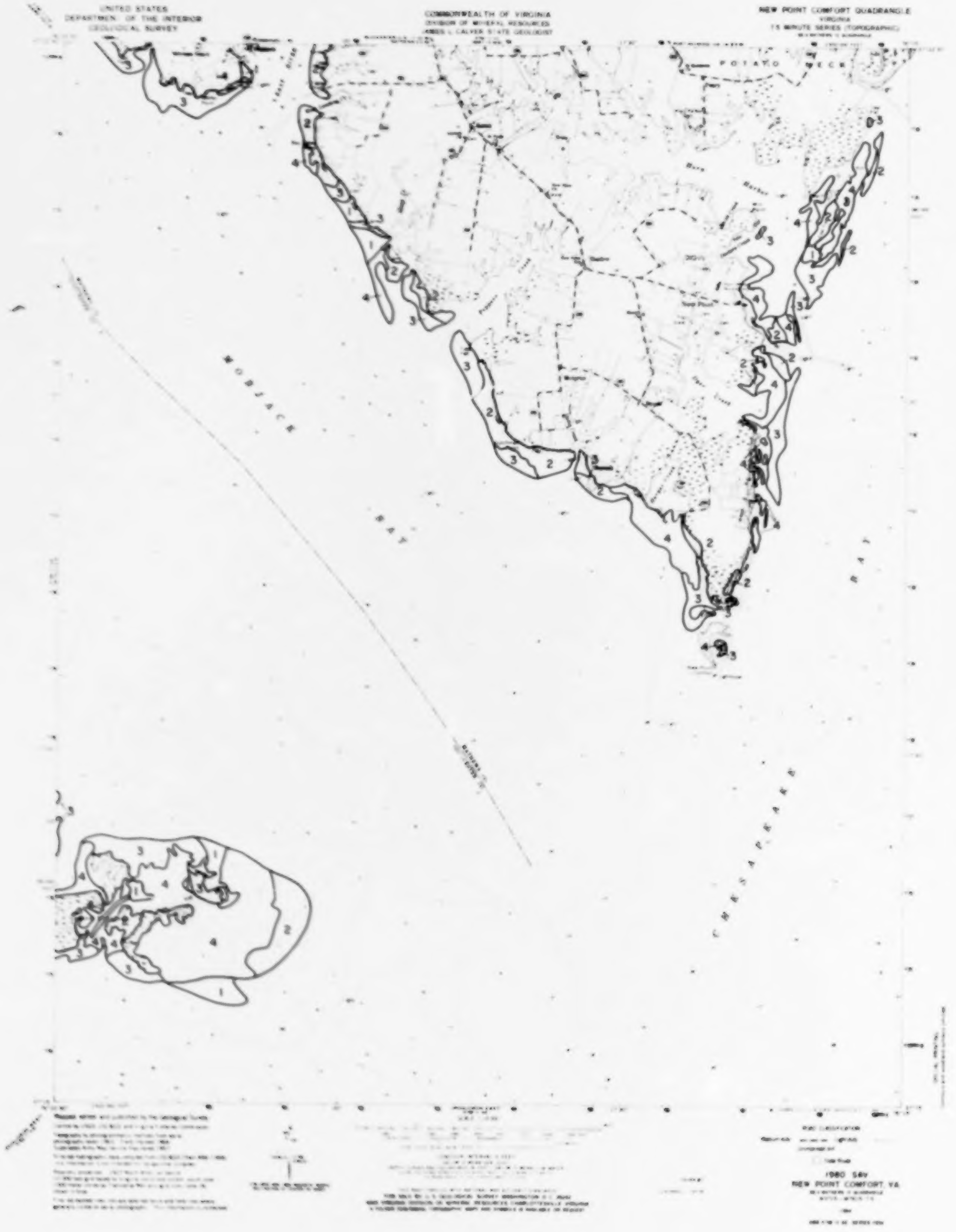
WARE NECK, VA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DIVISION OF MINERAL RESOURCES
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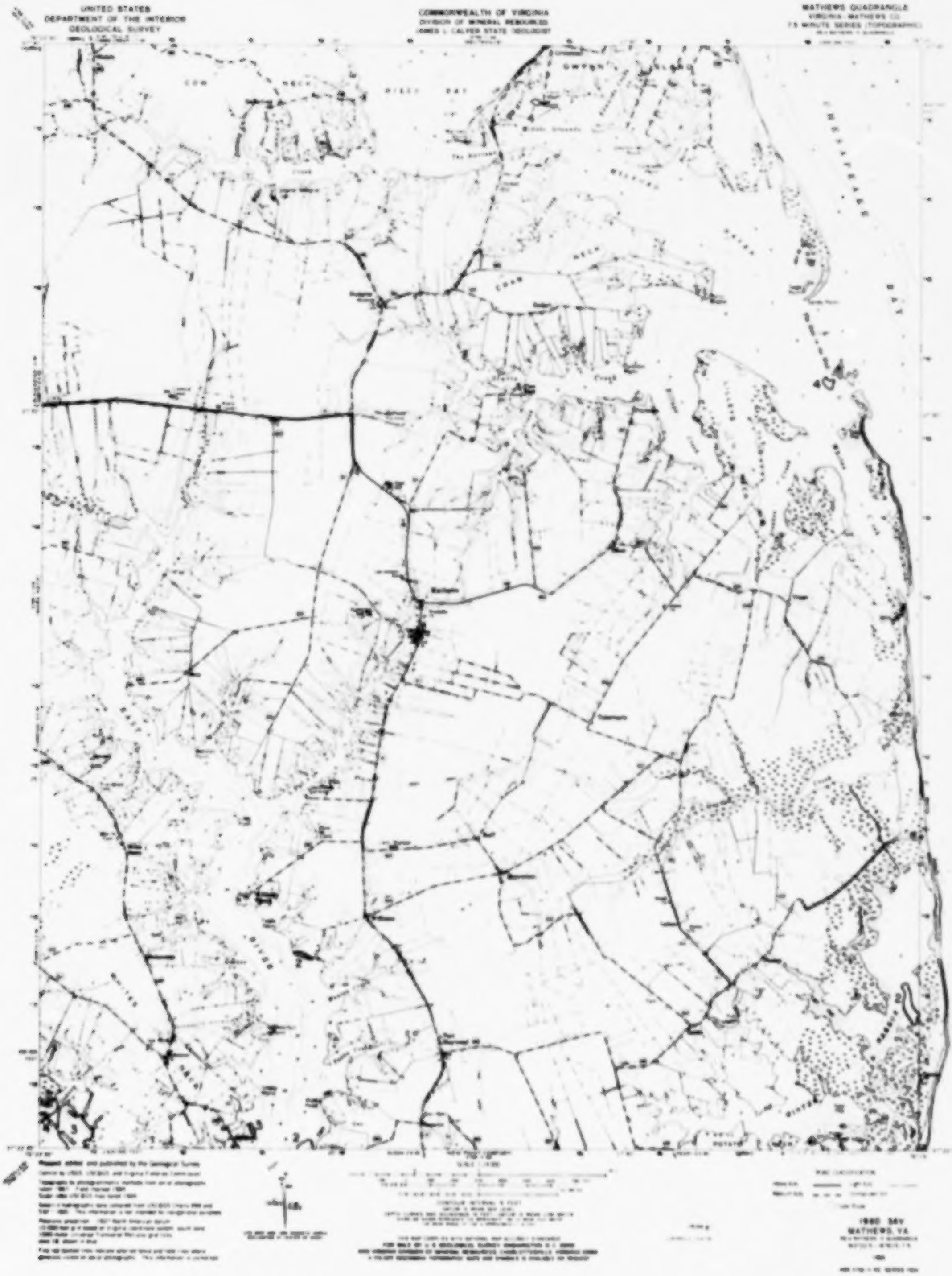
VIRGINIA
7.5 MINUTE SERIES (TOPOGRAPHIC)
POTATO NECK
MOBJACK BAY
CHESAPEAKE BAY
1
2
3
4
ROAD CLASSIFICATION
1980 S4V
NEW POINT COMFORT, VA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DIVISION OF MINERAL RESOURCES
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MATHEWS QUADRANGLE
VIRGINIA–MATHEWS CO.
7.5 MINUTE SERIES (TOPOGRAPHIC)
CHESAPEAKE
BAY
1980 SAV
MATHEWS, VA.

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DIVISION OF MINERAL RESOURCES
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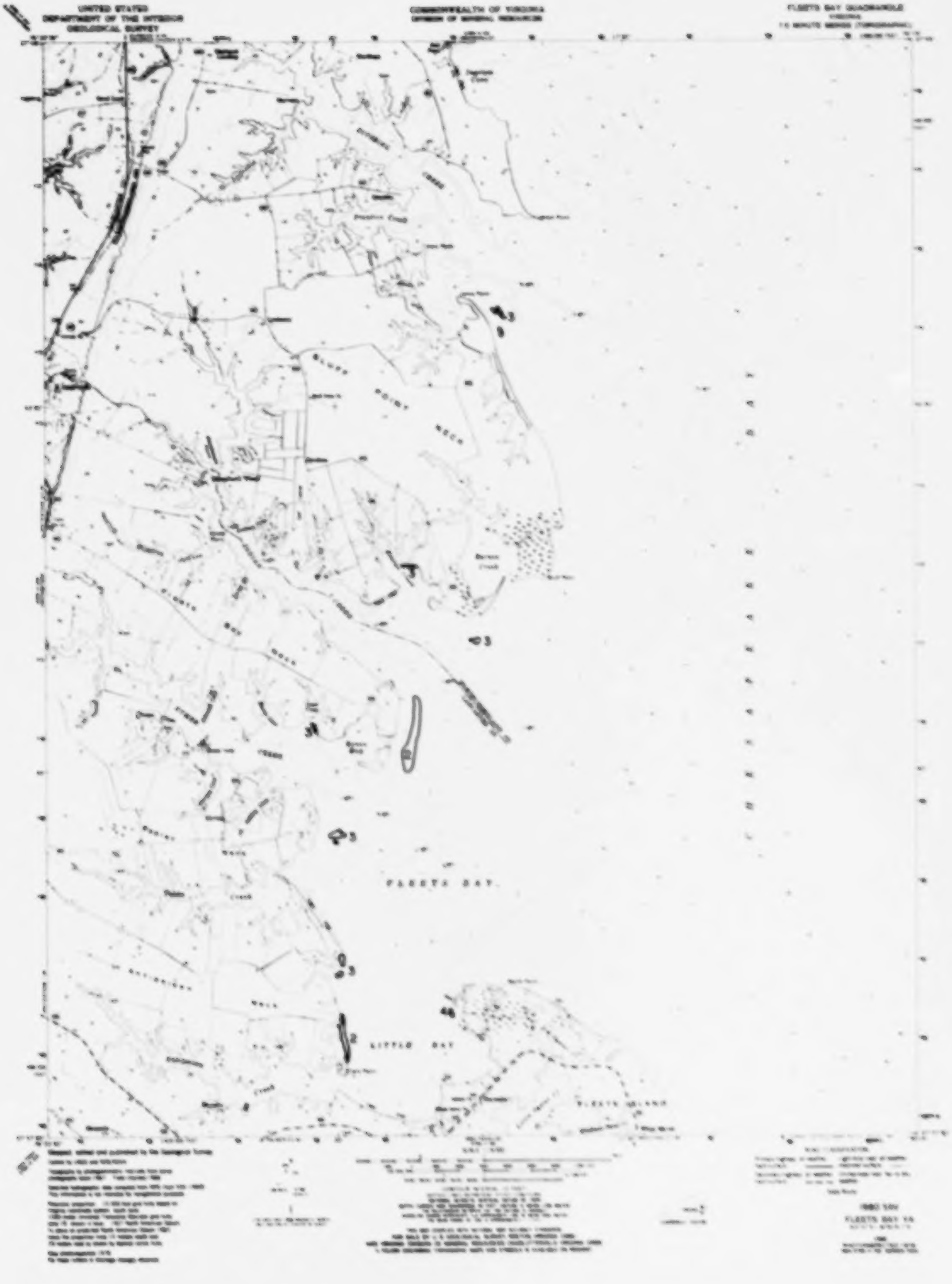
DELTAVILLE QUADRANGLE
VIRGINIA
7.5 MINUTE SERIES (TOPOGRAPHIC)
FLEETS ISLAND
RAPPAHANNOCK RIVER
CHESAPEAKE BAY
PIANKATANK RIVER
DELTAVILLE, VA.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FLEETS BAY QUADRANGLE
VIRGINIA
7.5 MINUTE SERIES (TOPOGRAPHIC)
FLEETS BAY
LITTLE BAY
FLEETS ISLAND
3
3
3
3
2
FLEETS BAY, VA.

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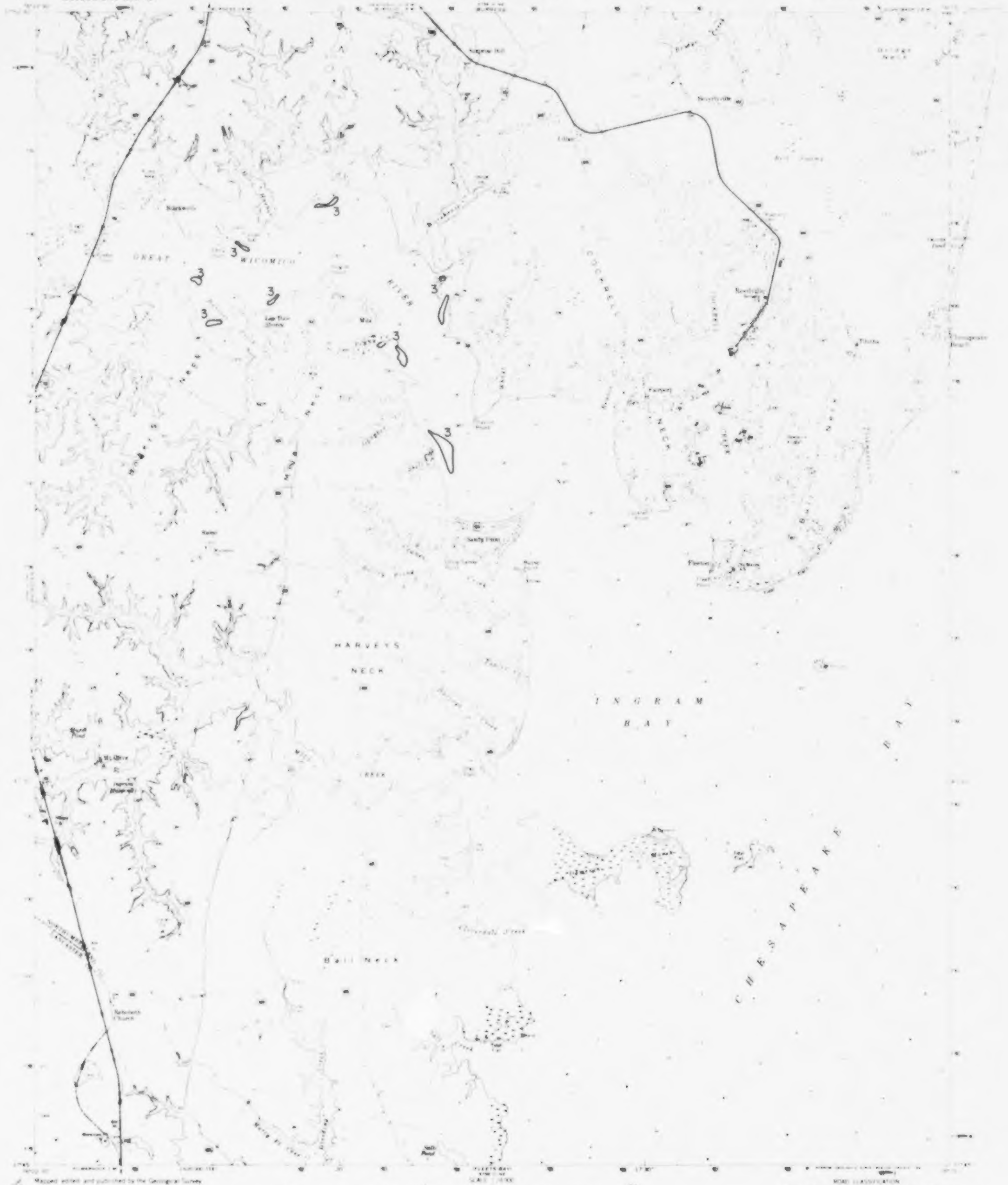
GEOLOGICAL SURVEY

COMMONWEALTH OF VIRGINIA
DIVISION OF MINERAL RESOURCES

REEDVILLE QUADRANGLE
VIRGINIA
7.5 MINUTE SERIES (TOPOGRAPHIC)



Mapped, edited, and published by the Geological Survey
Control by USGS and USC&GS
Topography by photogrammetric methods from aerial photographs taken 1967. Field checked 1968
Selected hydrographic data compiled from USC&GS chart 534 (1969). This information is not intended for navigational purposes
Polyconic projection. 10,000-foot grid ticks based on Virginia coordinate system, south zone
1000-meter Universal Transverse Mercator grid ticks, zone 18, shown in blue. 1927 North American Datum
To place on the predicted North American Datum 1983 move the projection lines 9 meters south and 29 meters east as shown by dashed corner ticks
Fine red dashed lines indicate selected fence and field lines where generally visible on aerial photographs. This information is unchecked

SCALE 1:24000

CONTOUR INTERVAL 10 FEET
DOTTED LINES REPRESENT 5-FOOT CONTOURS
NATIONAL GEODETIC VERTICAL DATUM OF 1929
DEPTH CURVES AND SOUNDINGS IN FEET—DATUM IS MEAN LOW WATER
THE RELATIONSHIP BETWEEN THE TWO DATUMS IS VARIABLE
SHORELINE SHOWN REPRESENTS THE APPROXIMATE LINE OF MEAN HIGH WATER
THE MEAN RANGE OF TIDE IS APPROXIMATELY 1 FOOT

THIS MAP COMPLIES WITH NATIONAL MAP ACCURACY STANDARDS
FOR SALE BY U. S. GEOLOGICAL SURVEY, RESTON, VIRGINIA 22092
AND VIRGINIA DIVISION OF MINERAL RESOURCES, CHARLOTTESVILLE, VIRGINIA 22903
A FOLDER DESCRIBING TOPOGRAPHIC MAPS AND SYMBOLS IS AVAILABLE ON REQUEST

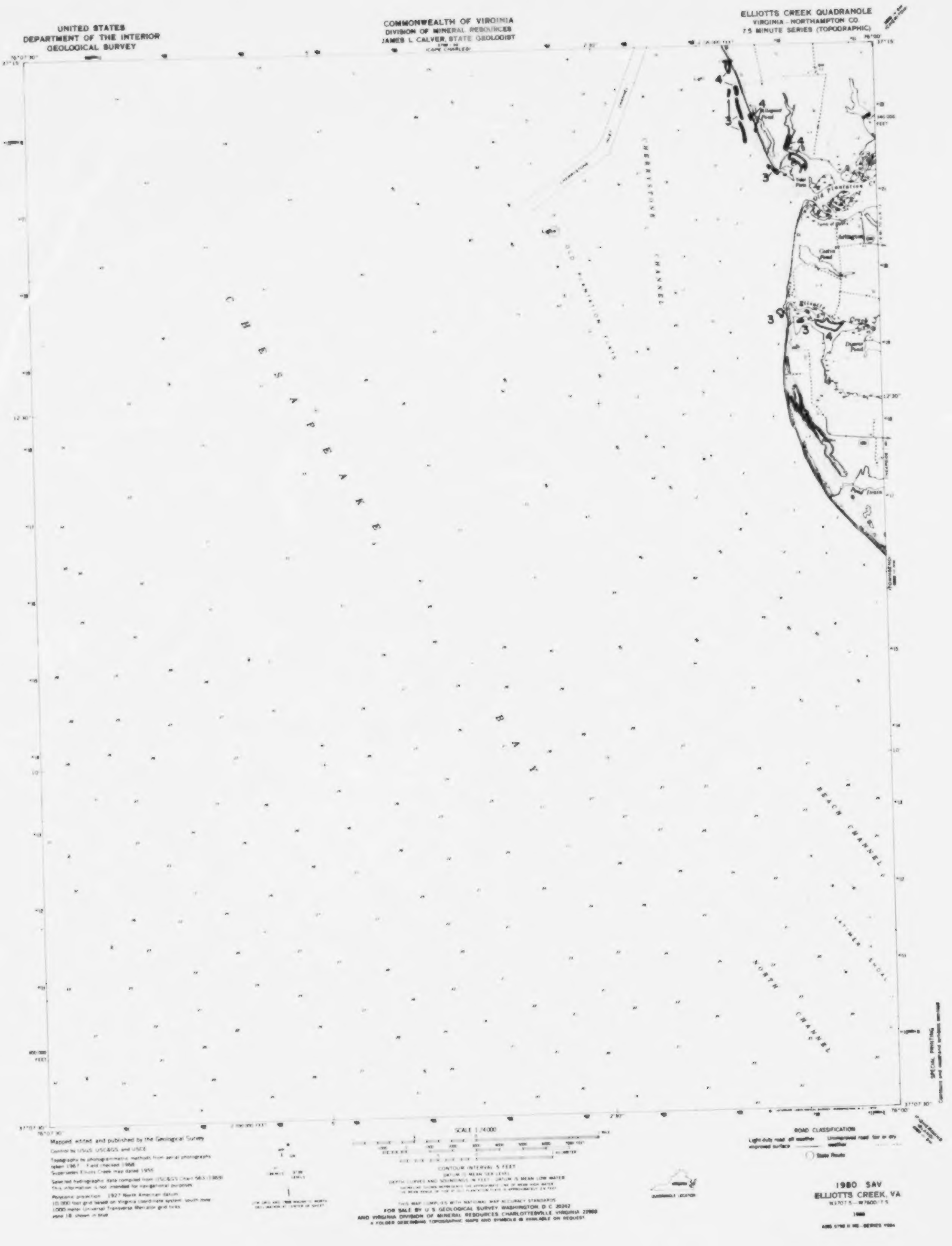
ROAD CLASSIFICATION
Primary highway, all weather, hard surface
Light-duty road, all weather, improved surface
Unimproved road, fair or dry weather
U. S. Route
State Route

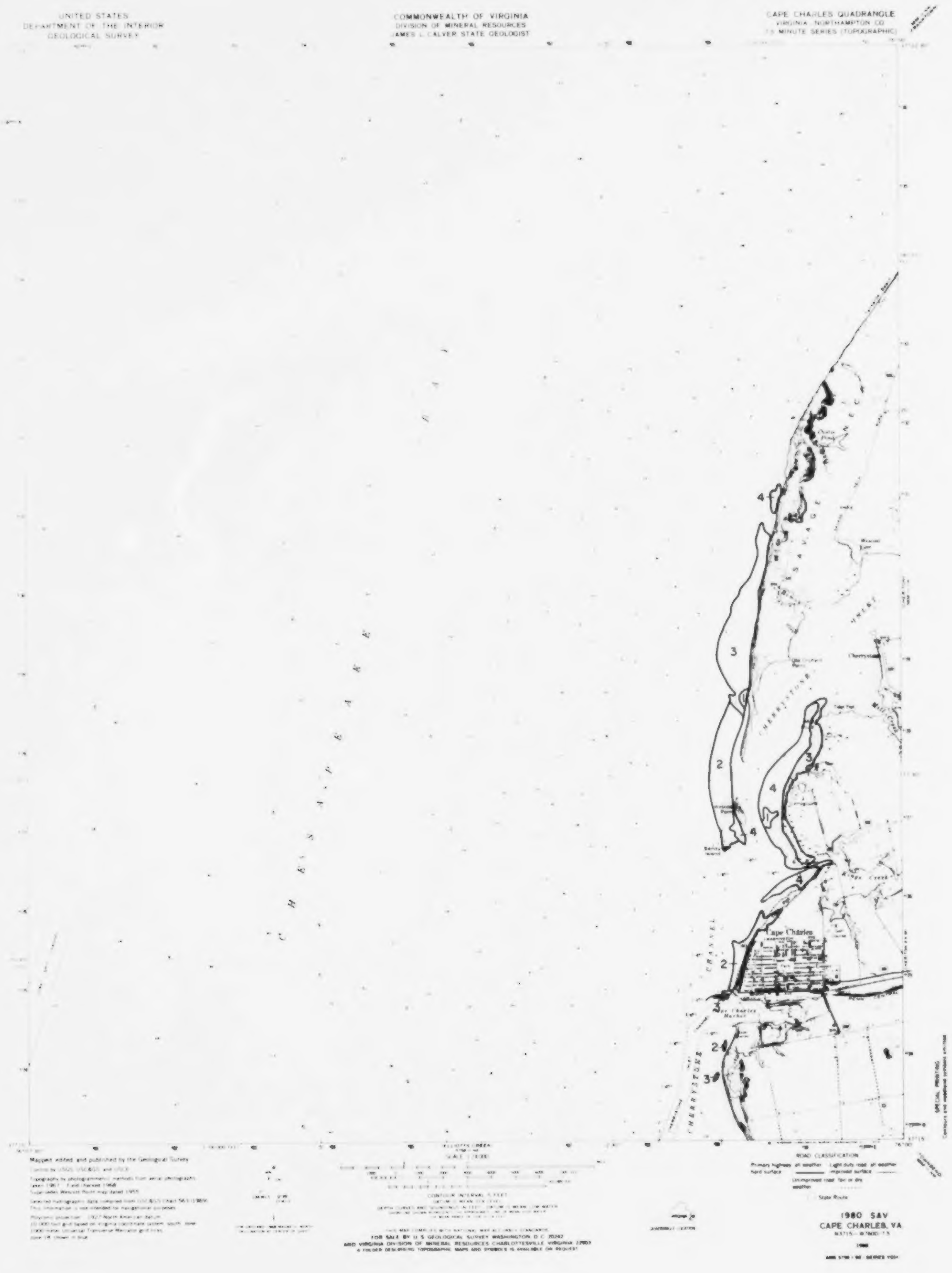
1980 SAV
REEDVILLE, VA

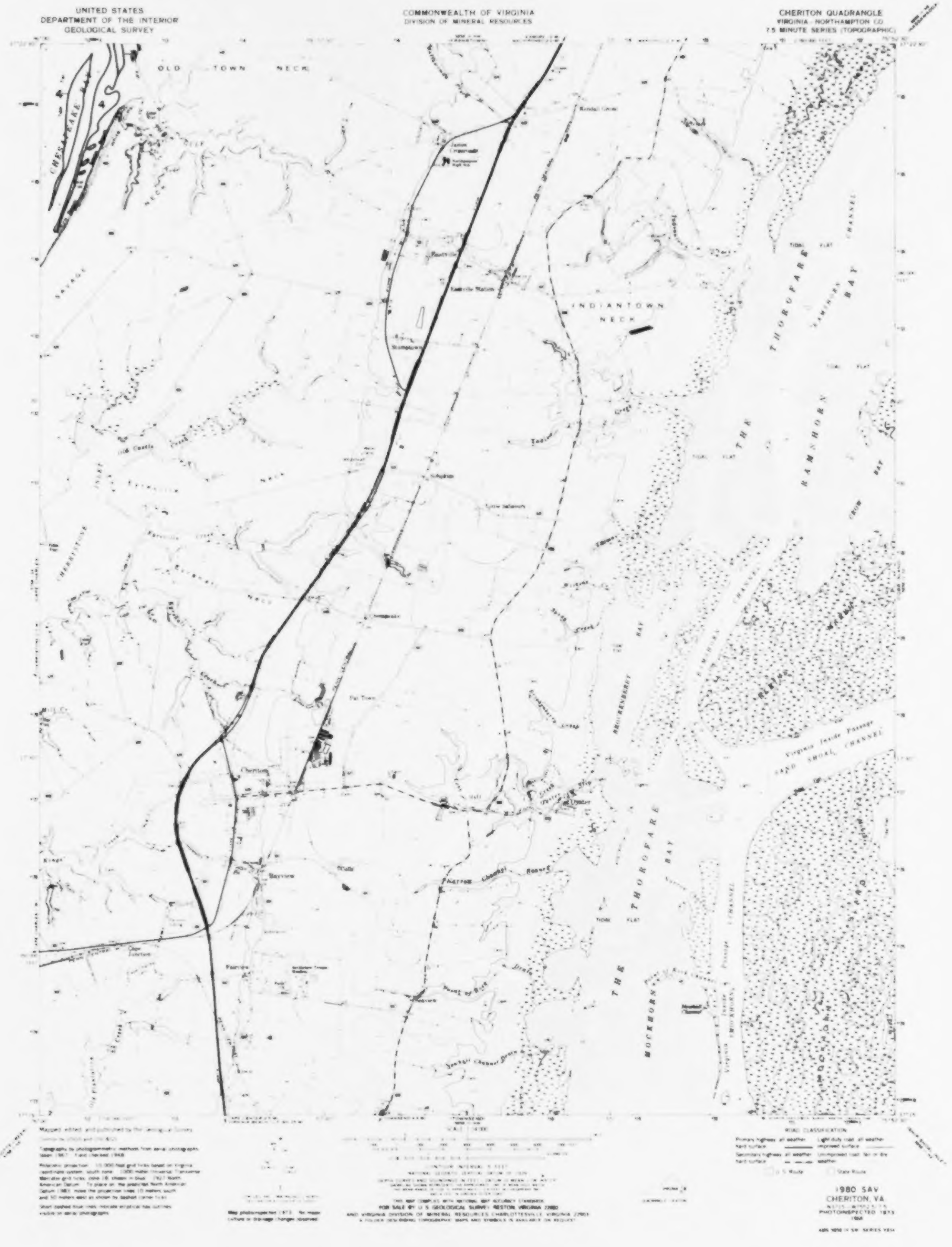
N3745—W7615/7.5

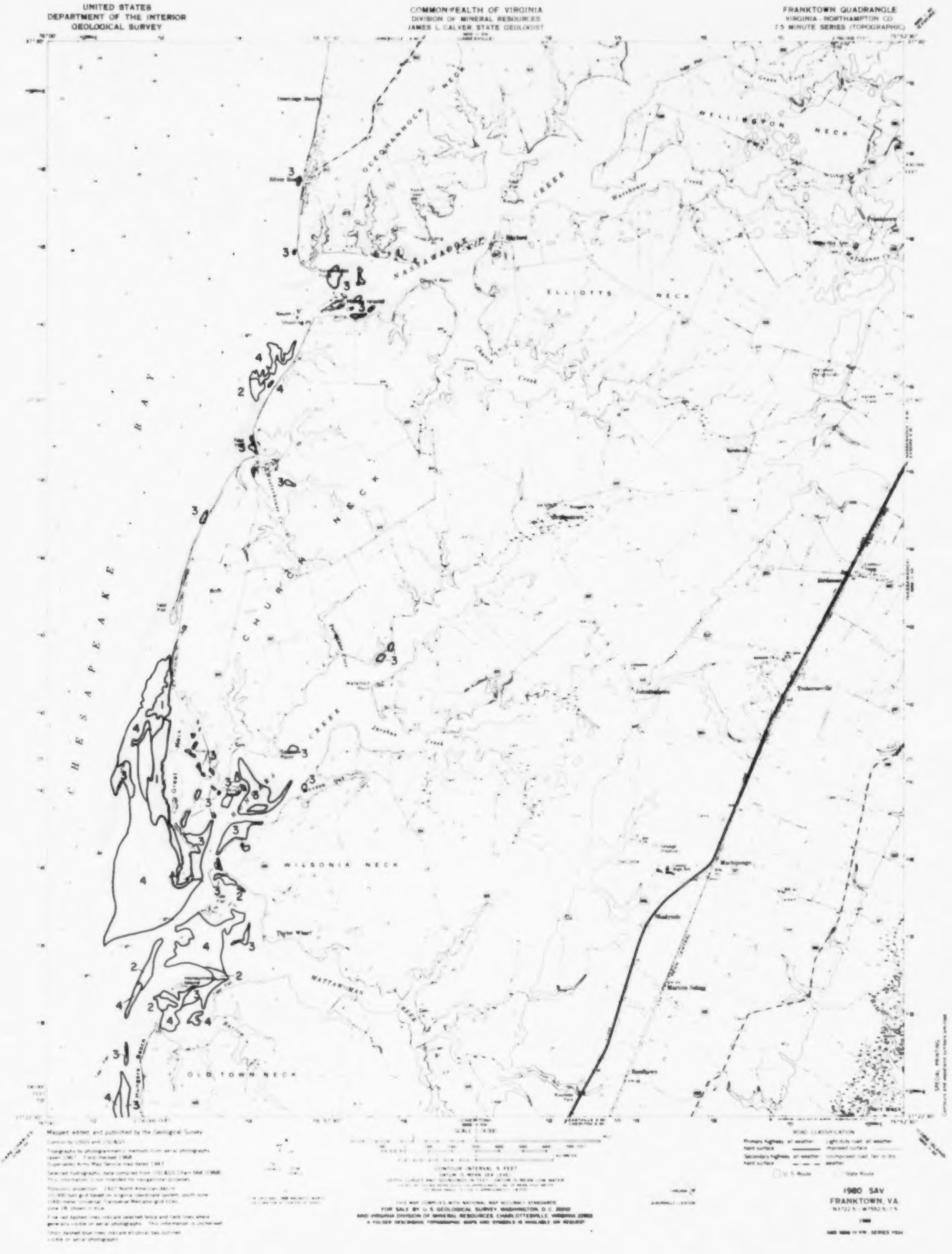
1968

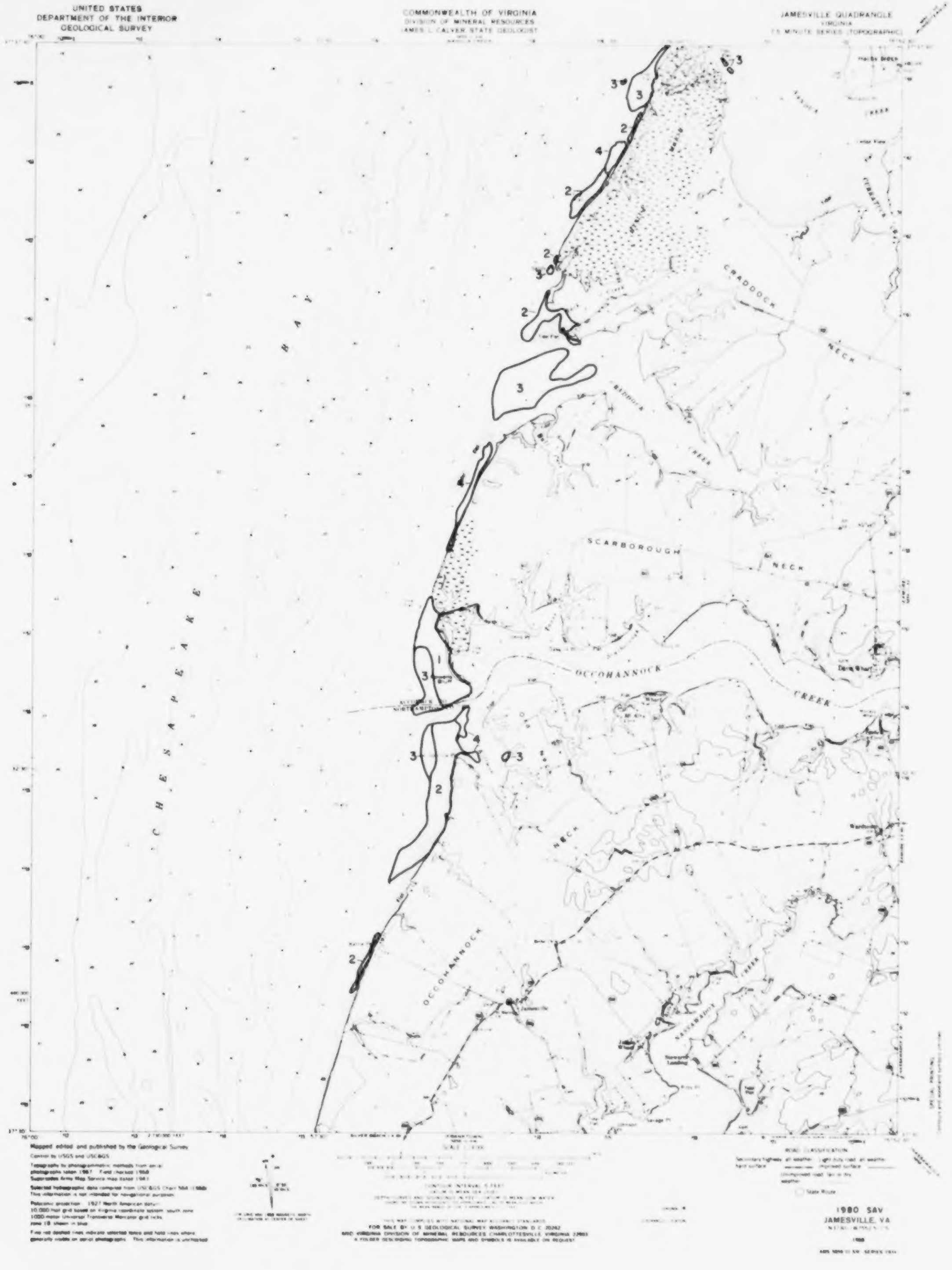
AMS 5761 IV SE—SERIES V834


UNITED STATES
DEPARTMENT OF THE INTERIOR
GEOLOGICAL SURVEY
COMMONWEALTH OF VIRGINIA
DIVISION OF MINERAL RESOURCES
JAMES L. CALVER, STATE GEOLOGIST
(CAPE CHARLES)
ELLIOTTS CREEK QUADRANGLE
VIRGINIA - NORTHAMPTON CO.
7.5 MINUTE SERIES (TOPOGRAPHIC)
CHESAPEAKE BAY
CHERRYSTONE CHANNEL
BEACH CHANNEL
LATIMER SHOAL
NORTH CHANNEL
3
4
Mapped, edited, and published by the Geological Survey
Control by USGS, USC&GS, and USCE
Topography by photogrammetric methods from aerial photographs taken 1967. Field checked 1968
Supersedes Elliotts Creek map dated 1955
Selected hydrographic data compiled from USC&GS Chart 563 (1969)
This information is not intended for navigational purposes
Polyconic projection. 1927 North American datum
10,000-foot grid based on Virginia coordinate system, south zone
1000-meter Universal Transverse Mercator grid ticks, zone 18, shown in blue
SCALE 1:24 000
CONTOUR INTERVAL 5 FEET
DATUM IS MEAN SEA LEVEL
DEPTH CURVES AND SOUNDINGS IN FEET - DATUM IS MEAN LOW WATER
THIS MAP COMPLIES WITH NATIONAL MAP ACCURACY STANDARDS
FOR SALE BY U. S. GEOLOGICAL SURVEY, WASHINGTON, D. C. 20242
AND VIRGINIA DIVISION OF MINERAL RESOURCES, CHARLOTTESVILLE, VIRGINIA 22903
A FOLDER DESCRIBING TOPOGRAPHIC MAPS AND SYMBOLS IS AVAILABLE ON REQUEST
ROAD CLASSIFICATION
Light-duty road, all weather, improved surface
Unimproved road, fair or dry weather
State Route
QUADRANGLE LOCATION
SPECIAL PRINTING
1980 SAV
ELLIOTTS CREEK, VA
N3707.5—W7600/7.5


UNITED STATES
DEPARTMENT OF THE INTERIOR
GEOLOGICAL SURVEY
COMMONWEALTH OF VIRGINIA
DIVISION OF MINERAL RESOURCES
JAMES L. CALVER STATE GEOLOGIST
CAPE CHARLES QUADRANGLE
VIRGINIA–NORTHAMPTON CO.
7.5 MINUTE SERIES (TOPOGRAPHIC)
CHESAPEAKE BAY
CHERRYSTONE
CHANNEL
Cape Charles
4
3
2
4
3
4
4
2
3
2
4
3
ROAD CLASSIFICATION
Primary highway, all weather, hard surface
Light-duty road, all weather, improved surface
Unimproved road, fair or dry weather
State Route
SPECIAL PRINTING
1980 SAV
CAPE CHARLES, VA


UNITED STATES
DEPARTMENT OF THE INTERIOR
GEOLOGICAL SURVEY
COMMONWEALTH OF VIRGINIA
DIVISION OF MINERAL RESOURCES
CHERITON QUADRANGLE
VIRGINIA - NORTHAMPTON CO.
7.5 MINUTE SERIES (TOPOGRAPHIC)
OLD TOWN NECK
CHESAPEAKE BAY
Kendall Grove
Eastville
Eastville Station
INDIANTOWN NECK
THE THOROFARE
RAMSHORN BAY
TIDAL FLAT
THE RAMSHORN
Old Castle Creek
Cheriton
Bayview
Cape Charles
Virginia Inside Passage
SAND SHOAL CHANNEL
BRUCKENBERRY BAY
THE THOROFARE
MOCKHORN BAY
THE
ROAD CLASSIFICATION
Primary highway, all weather, hard surface
Light-duty road, all weather, improved surface
Secondary highway, all weather, hard surface
Unimproved road, fair or dry weather
U.S. Route
State Route
1980 SAV
CHERITON, VA
PHOTOINSPECTED 1973
1968


UNITED STATES
DEPARTMENT OF THE INTERIOR
GEOLOGICAL SURVEY
COMMONWEALTH OF VIRGINIA
DIVISION OF MINERAL RESOURCES
JAMES L. CALVER, STATE GEOLOGIST
FRANKTOWN QUADRANGLE
VIRGINIA - NORTHAMPTON CO.
7.5 MINUTE SERIES (TOPOGRAPHIC)
CHESAPEAKE BAY
OCCOHANNOCK NECK
NASSAWADOX CREEK
WELLINGTON NECK
ELLIOTTS NECK
CHURCH NECK
WILSONIA NECK
MATTAWOMAN CREEK
OLD TOWN NECK
Jacobus Creek
CONTOUR INTERVAL 5 FEET
ROAD CLASSIFICATION
Primary highway, all weather, hard surface
Secondary highway, all weather, hard surface
Light-duty road, all weather, improved surface
Unimproved road, fair or dry weather
U. S. Route
State Route
1980 SAV
FRANKTOWN, VA
1
2
3
4
0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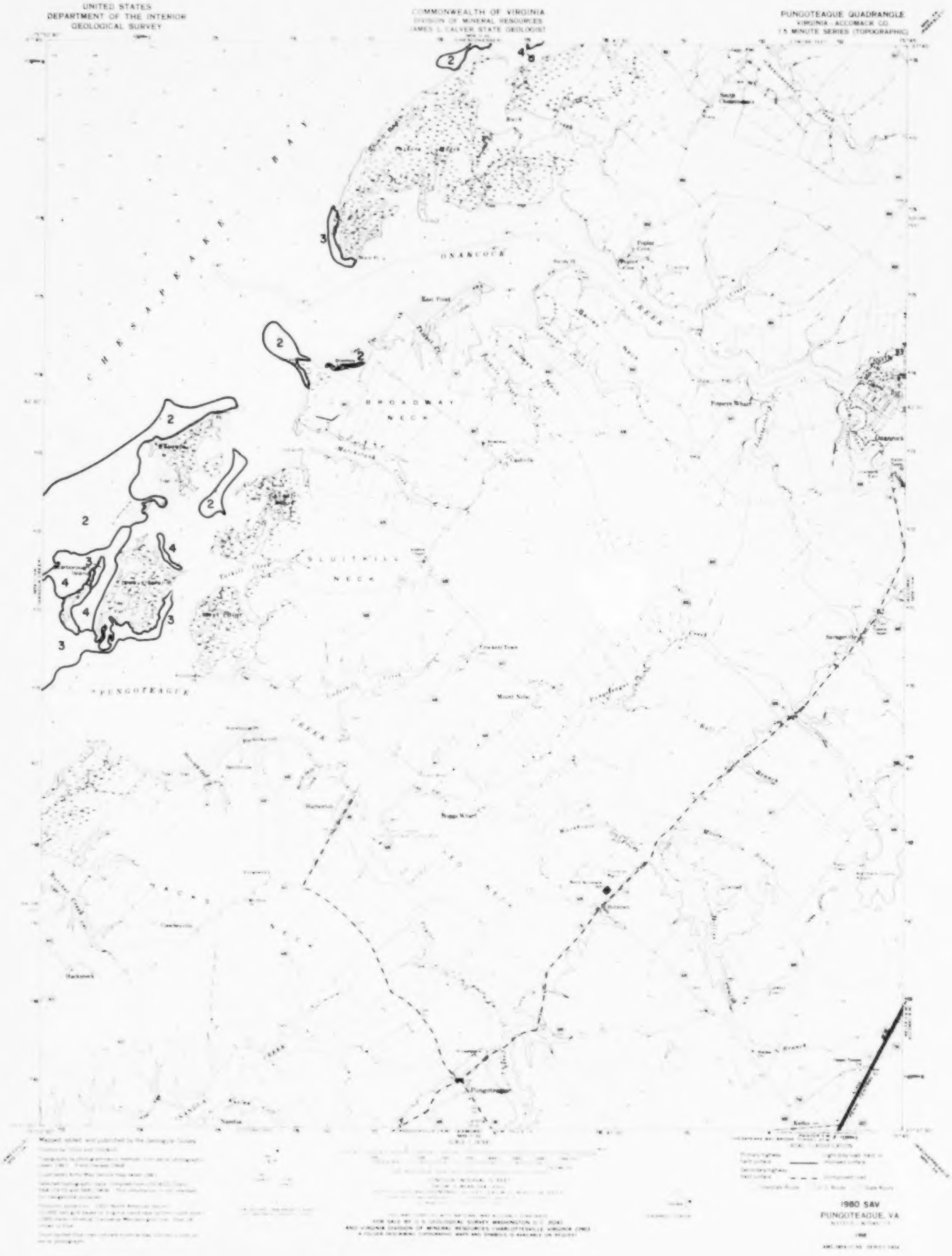
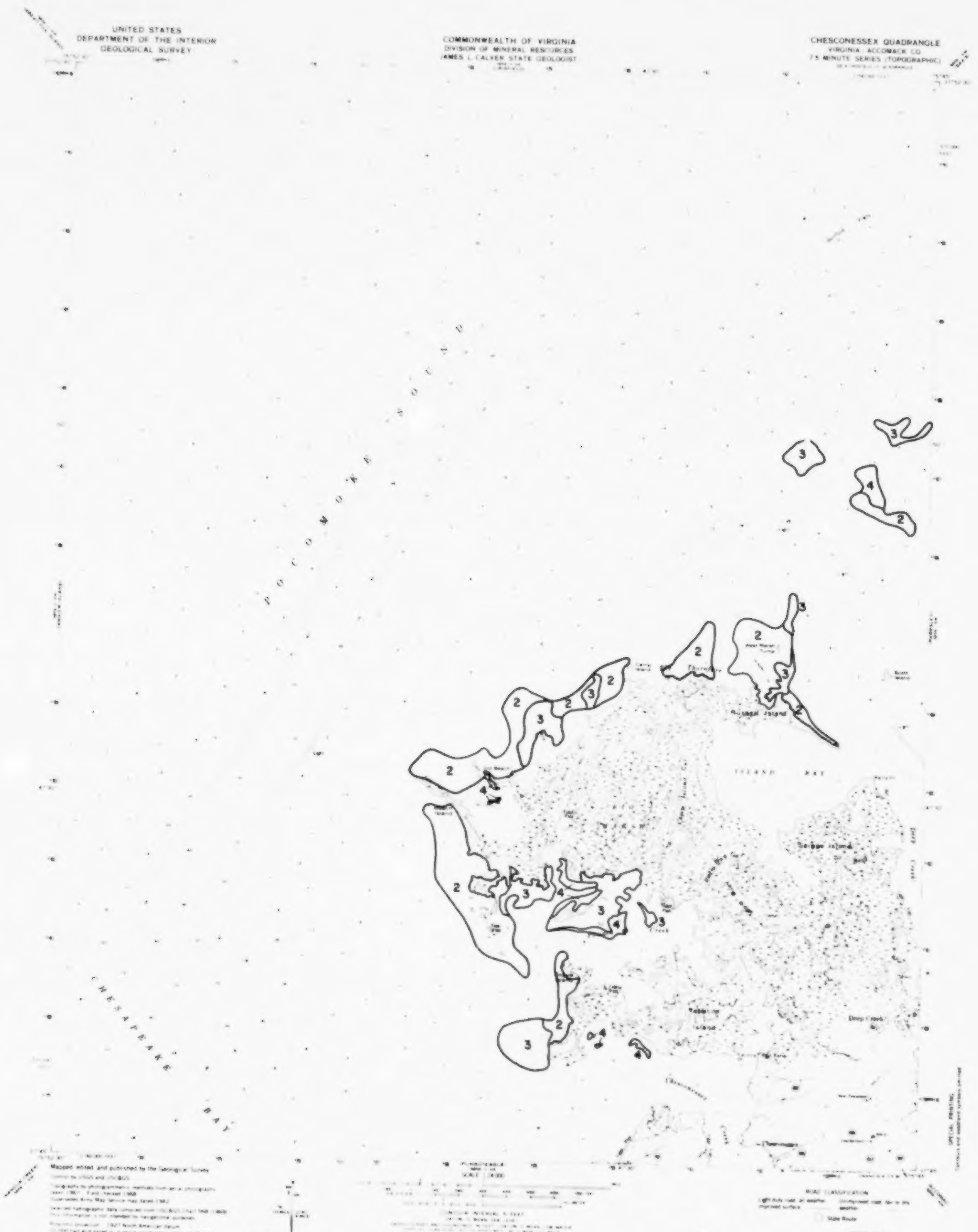
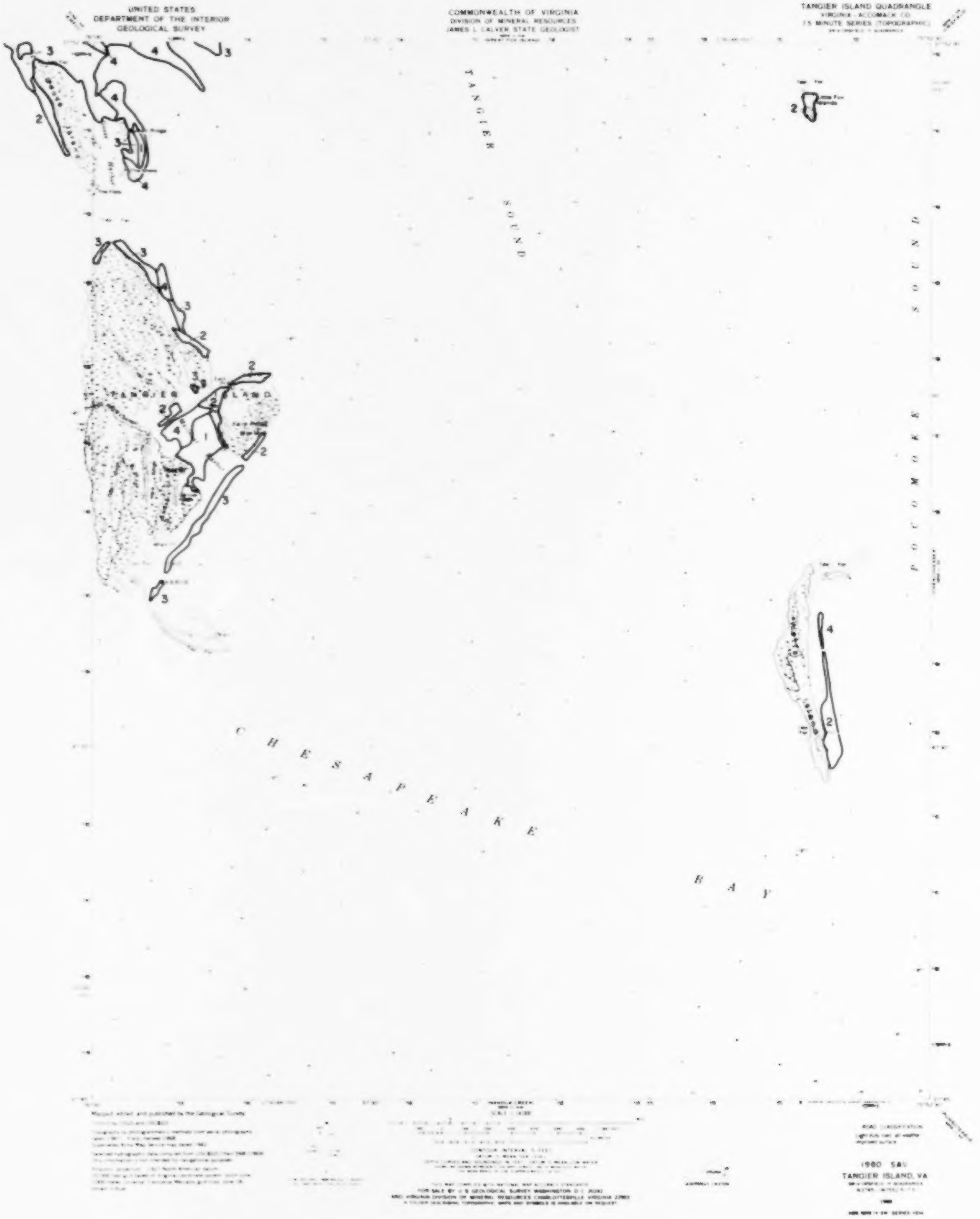
DEPARTMENT OF THE INTERIOR
GEOLOGICAL SURVEY
COMMONWEALTH OF VIRGINIA
DIVISION OF MINERAL RESOURCES
JAMES L. CALVER STATE GEOLOGIST
JAMESVILLE QUADRANGLE
VIRGINIA
7.5 MINUTE SERIES (TOPOGRAPHIC)
CHESAPEAKE BAY
CRADDOCK NECK
SCARBOROUGH NECK
OCCOHANNOCK CREEK
OCCOHANNOCK NECK
Jamesville
1
2
3
4
Mapped, edited, and published by the Geological Survey
Control by USGS and USC&GS
Topography by photogrammetric methods from aerial photographs taken 1967. Field checked 1968
Supersedes Army Map Service map dated 1943
Selected hydrographic data compiled from USC&GS Chart 564 (1968)
This information is not intended for navigational purposes
Polyconic projection. 1927 North American datum
10,000-foot grid based on Virginia coordinate system, south zone
1000-meter Universal Transverse Mercator grid ticks, zone 18, shown in blue
Fine red dashed lines indicate selected fence and field lines where generally visible on aerial photographs. This information is unchecked
SCALE 1:24 000
CONTOUR INTERVAL 5 FEET
DATUM IS MEAN SEA LEVEL
THIS MAP COMPLIES WITH NATIONAL MAP ACCURACY STANDARDS
FOR SALE BY U. S. GEOLOGICAL SURVEY, WASHINGTON, D. C. 20242
AND VIRGINIA DIVISION OF MINERAL RESOURCES, CHARLOTTESVILLE, VIRGINIA 22903
A FOLDER DESCRIBING TOPOGRAPHIC MAPS AND SYMBOLS IS AVAILABLE ON REQUEST
ROAD CLASSIFICATION
Secondary highway, all weather, hard surface
Light-duty road, all weather, improved surface
Unimproved road, fair or dry weather
State Route
1980 SAV
JAMESVILLE, VA
1968

UNITED STATES
DEPARTMENT OF THE INTERIOR
GEOLOGICAL SURVEY
COMMONWEALTH OF VIRGINIA
DIVISION OF MINERAL RESOURCES
JAMES L. CALVER STATE GEOLOGIST
NANDUA CREEK QUADRANGLE
VIRGINIA–ACCOMACK CO.
7.5 MINUTE SERIES (TOPOGRAPHIC)
CHESAPEAKE
BAY
2
3
4
NANDUA
CREEK
Mapped, edited, and published by the Geological Survey
CONTOUR INTERVAL 5 FEET
ROAD CLASSIFICATION
Light-duty road, all weather, improved surface
Unimproved road, fair or dry weather
NANDUA CREEK, VA.
AMS 5858 III NW–SERIES V834

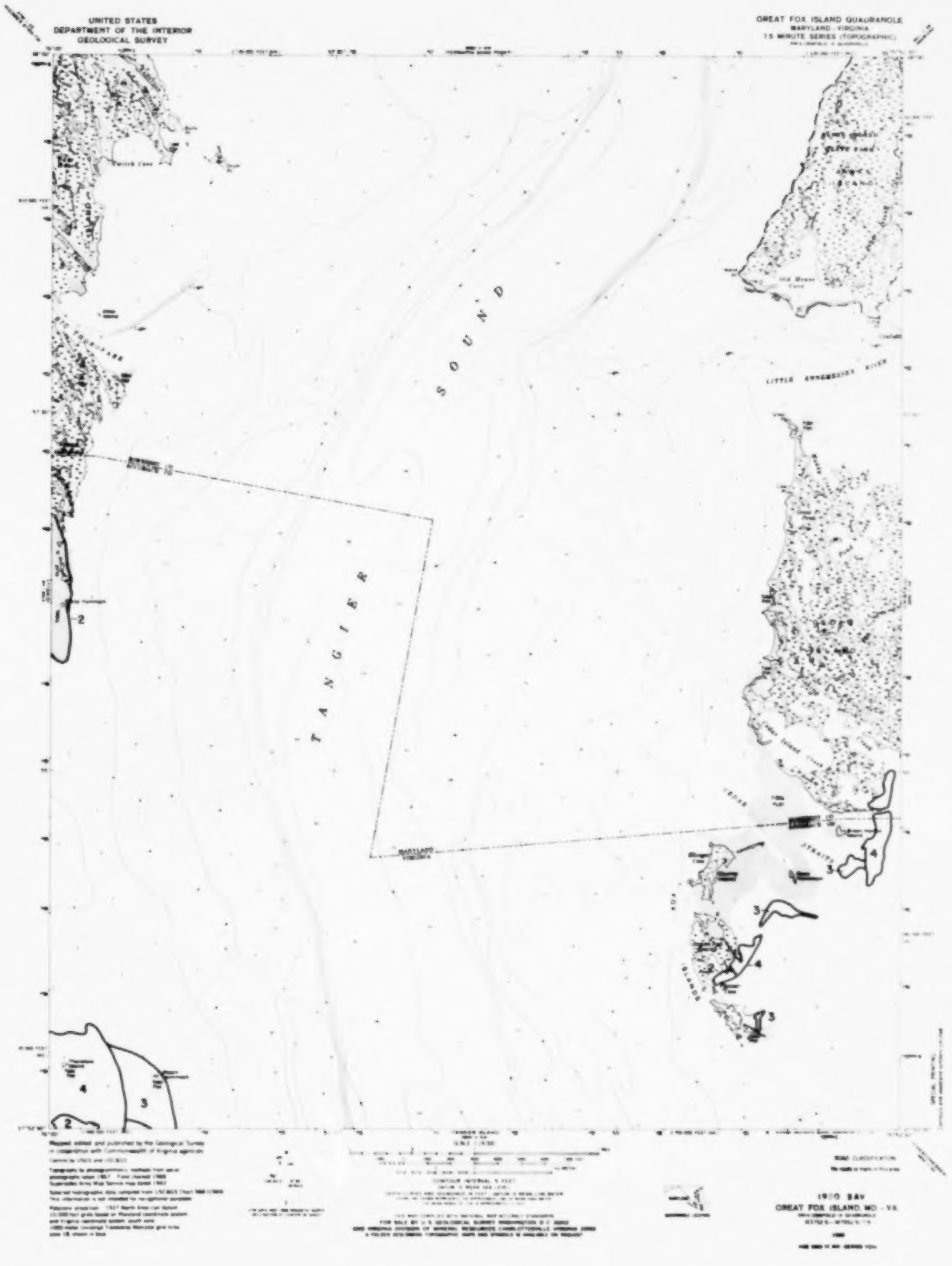

UNITED STATES
DEPARTMENT OF THE INTERIOR
GEOLOGICAL SURVEY
COMMONWEALTH OF VIRGINIA
DIVISION OF MINERAL RESOURCES
JAMES L. CALVER STATE GEOLOGIST
PUNGOTEAGUE QUADRANGLE
VIRGINIA - ACCOMACK CO.
7.5 MINUTE SERIES (TOPOGRAPHIC)
CHESAPEAKE BAY
ONANCOCK
CREEK
BROADWAY NECK
SLUITKILL NECK
PUNGOTEAGUE
CREEK
East Point
Finneys Wharf
Onancock
Savageville
Crockett Town
Mount Nebo
Boggs Wharf
Harborton
Hacksneck
Nandua
Pungoteague
Keller
2
3
4
ROAD CLASSIFICATION
Primary highway, hard surface
Secondary highway, hard surface
Light-duty road, hard or improved surface
Unimproved road
Interstate Route
U.S. Route
State Route
1980 SAV
PUNGOTEAGUE, VA


UNITED STATES
DEPARTMENT OF THE INTERIOR
GEOLOGICAL SURVEY
COMMONWEALTH OF VIRGINIA
DIVISION OF MINERAL RESOURCES
JAMES L. CALVER STATE GEOLOGIST
CHESCONESSEX QUADRANGLE
VIRGINIA - ACCOMACK CO.
7.5 MINUTE SERIES (TOPOGRAPHIC)
POCOMOKE SOUND
CHESAPEAKE BAY
ISLAND BAY
Russell Island
Deep Creek
3
3
4
2
2
3
2
3
2
3
2
2
3
3
2
4
2
3
4
3
4
3
2
3
4
Mapped, edited, and published by the Geological Survey
SCALE 1:24000
CONTOUR INTERVAL 5 FEET
ROAD CLASSIFICATION
Light-duty road, all weather, improved surface
Unimproved road, fair or dry weather
State Route
1980 SAV
CHESCONESSEX, VA
SPECIAL PRINTING

UNITED STATES
DEPARTMENT OF THE INTERIOR
GEOLOGICAL SURVEY
COMMONWEALTH OF VIRGINIA
DIVISION OF MINERAL RESOURCES
JAMES L. CALVER, STATE GEOLOGIST
PARKSLEY QUADRANGLE
3
3
3
4
3
2
3
3
Parksley
High Hook
1980 SAV
PARKSLEY, VA.


UNITED STATES
DEPARTMENT OF THE INTERIOR
GEOLOGICAL SURVEY
COMMONWEALTH OF VIRGINIA
DIVISION OF MINERAL RESOURCES
JAMES L. CALVER STATE GEOLOGIST
TANGIER ISLAND QUADRANGLE
VIRGINIA - ACCOMACK CO.
7.5 MINUTE SERIES (TOPOGRAPHIC)
TANGIER SOUND
POCOMOKE SOUND
TANGIER ISLAND
CHESAPEAKE BAY
1
2
3
4
Mapped, edited, and published by the Geological Survey
CONTOUR INTERVAL 5 FEET
FOR SALE BY U S GEOLOGICAL SURVEY WASHINGTON D C 20242
AND VIRGINIA DIVISION OF MINERAL RESOURCES CHARLOTTESVILLE VIRGINIA 22903
A FOLDER DESCRIBING TOPOGRAPHIC MAPS AND SYMBOLS IS AVAILABLE ON REQUEST
ROAD CLASSIFICATION
Light duty road, all weather improved surface
1980 SAV
TANGIER ISLAND, VA
1968

UNITED STATES
DEPARTMENT OF THE INTERIOR
GEOLOGICAL SURVEY
EWELL QUADRANGLE
MARYLAND–VIRGINIA
7.5 MINUTE SERIES (TOPOGRAPHIC)
SMITH ISLAND
CHESAPEAKE BAY
1
2
3
4
1980 SAV
EWELL, MD.–VA.



UNITED STATES
DEPARTMENT OF THE INTERIOR
GEOLOGICAL SURVEY
GREAT FOX ISLAND QUADRANGLE
MARYLAND - VIRGINIA
7.5 MINUTE SERIES (TOPOGRAPHIC)
SOUND
TANGIER
LITTLE ANNEMESSEX RIVER
MARYLAND
VIRGINIA
1
2
3
4
CONTOUR INTERVAL 5 FEET
DATUM IS MEAN SEA LEVEL
ROAD CLASSIFICATION
1970 SAV
GREAT FOX ISLAND, MD - VA

SECTION II

INTERACTIVE EFFECTS OF LIGHT, EPIPHYTES AND GRAZERS

CHAPTER 1

EPIPHYTE-SEAGRASS RELATIONSHIPS WITH AN EMPHASIS ON THE ROLE OF MICROGRAZING: A REVIEW[1]

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and
Jacques van Montfrans

Virginia Institute of Marine Science
and
School of Marine Science
of the College of William and Mary
Gloucester Point, Virginia 23062

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[1] Contribution No. 1040 from the Virginia Institute of Marine Science

ABSTRACT

Despite the recent advances in seagrass ecology over the last 10 years, there are still numerous aspects on the ecological and biological interactions that occur in seagrass ecosystems that remain poorly understood. We have attempted to place into perspective one interrelationship that could have important implications in the production and vigor of seagrasses. This is the relationship between epiphytic fouling by macroalgae and periphyton and the grazers which consume them as a food source while leaving the leaves intact. Our approach to this review was to first describe the relationships between macroalgae, periphyton and the seagrass host in terms of physical benefits, biochemical interactions, factors which reduce fouling on the host and effects of epiphytism on seagrass photosynthesis. We then examined the importance of epiphytes as a food source for those herbivores found in seagrass beds and then looked at the consequences of this grazing and removal of epiphytes for the seagrass host. Based on the potential impact of epiphytes on seagrasses and grazers on epiphytes, we developed a hypothetical model that describes the effect of increasing epiphytic fouling on seagrass production in the presence and absence of grazers. From this model, we made predictions on the direction of seagrass decline with diminishing light along depth and estuarine gradients. Lastly, we briefly touched on the problem of eutrophication and how it affects the balance of these interrelationships and the management options to insure the health and survival of seagrass habitats in the face of increasing stress by man on these critically important areas.

INTRODUCTION

Recent emphasis on seagrass research has shifted from a primarily descriptive approach to attempt to understand the functional ecology of such habitats. Books containing review papers on seagrass ecosystems (McRoy and Helfferich, 1977; Phillips and McRoy, 1980) as well as the large number of articles appearing in many scientific and popular journals, attest to the progress made in understanding seagrass habitats on a worldwide basis. There are, however, numerous aspects of the functional ecology of these complex systems that still remain poorly understood. One such area involves the interrelationship between epiphytic fouling by both macroalgae and periphyton (loosely defined here as the community of diatoms, microfauna and particulate material [Weitzel, 1979]) adhering to seagrass blades and the grazing organisms which rely on these as important food sources. The grazing community associated with seagrasses consists of a variety of organisms whose activities range from consumption of the leaf blade with the epiphytes to removal of only the epiphytic assemblage. We have limited our discussion to grazers, such as gastropods, crustaceans and some species of fish, which consume only macroalgae and/or periphyton found on the surface of the leaf blade while leaving the leaf intact.

The main emphasis of this review concentrates on the: 1) relationships between macroalgae, periphyton and the seagrasses which they colonize; 2) importance of epiphytes as a food source for numerous herbivores found in seagrass beds; 3) consequences of grazing on epiphytes for the host plant; and 4) ways in which eutrophication affects the balance of these complex interrelationships. We will also briefly touch on the management implications of these interrelationships for the health and survival of seagrass habitats based on the current level of knowledge.

I. EPIPHYTE-SEAGRASS RELATIONSHIPS

Seagrasses grow in a variety of sediment types in shallow water and frequently provide the only available solid substrate for the attachment of macroalgae (Humm, 1973). Their presence can increase the surface area of the bottom available for colonization by epiphytic or epibenthic diatoms by a factor of 5 to almost 19 (Kita and Harada, 1962; Reyes-Vasquez, 1970; Gessner, 1974). The total primary productivity of the seagrass habitat is substantially increased (Wood et al., 1969) because seagrass provides a suitable substrate for other photosynthetic organisms.

A diverse assemblage of microflora and macroflora is associated with the seagrass blades (Harlin, 1980). The presence of these organisms on these blades results from a number of complex interrelationships that not only have important implications for the growth of the seagrass but also may have led to the evolution of internal mechanisms to suppress epiphytic growth. For the purpose of discussion, we have divided the relationships into those which a) provide physical benefits to the epiphyte or seagrass, b) involve biochemical interactions, c) are concerned with factors which reduce fouling, and d) involve implications of epiphytism on seagrass photosynthesis.

a. Beneficial Effects of the Relationship: Physical

Few beneficial effects for seagrasses of this epiphyte-host-relationship have been discussed in the literature. Penhale and Smith (1977) suggested that the presence of epiphytes can reduce the effects of desiccation when *Zostera marina* is exposed at low tide. Richardson (1980) surmised that seeds of *Ruppia maritima* which were released under mats of epiphytic algae were more resistant to desiccation when water levels dropped and the exposed seeds were protected from drying out by the overlying algae. *Halophilia engelmanni* was found to have a low tolerance to ultraviolet-B radiation and it was postulated that *H. engelmanni* relied on periphyton shielding as well as shade provided by other seagrasses to reduce photoinhibition (Trocine et al., 1981). Its congener *Halophilia stipulacea* also exhibited photoinhibition at lower light intensities than *Cymodocea nodosa*, *Phyllospadix torreyi*, *Posidonia oceanica*, *Zostera angustifolia* and *Z. marina* (Drew, 1979). Perhaps the former species relies on shading by epiphytes and surrounding vegetation to reduce light intensities as well.

Epiphytes of submerged vascular plants are believed to benefit from the association by their enhanced proximity to light and water currents carrying dissolved nutrients (Harlin, 1980). The swaying motion of seagrasses caused by wave action and currents may be important in producing steep chemical diffusion gradients and removing potential growth inhibiting substances as well as accumulated sediments. The results of this physical movement alone enhances the exchange of nutrients and epiphytic growth (Conover, 1968; Harlin, 1975, 1980).

b. Biochemical Interactions

Several studies have been conducted which enumerate the diverse macro- and microflora assemblages associated with submerged vegetation (Harlin, 1980, partial review). Although some macroalgal species (e.g. *Punctaria orbiculata* and *Smithora naiadum*) are believed to be more dependent on their macrophyte host for the completion of their life cycle (Harlin, 1975), the vast majority are thought to merely utilize the host as a substrate for attachment. Similarly, most diatom species found on marine angiosperms are classified as obligate epiphytes (McIntire and Moore, 1977) although their occurrence is by no means restricted only to angiosperms (Brown, 1962; Main and McIntire, 1974; Jacobs and Noten, 1980). Some diatom assemblages of macrophytes were found to be essentially the same as those colonizing the surrounding bottom (Sullivan, 1977). It is likely, however, that under nutrient limited conditions, microalgae, such as unicellular diatoms, which are more intimately associated with the macrophyte host epithelium, are influenced to a greater extent by host metabolism (and vice versa) than the larger multicellular erect forms. Because of their large surface area to volume ratio, unicells have a more intimate relationship with their microcellular plants (Wood, 1972). This fact may be partially responsible for the observation that periphyton productivity or biomass have been shown to track that of the seagrass substrate (Penhale, 1977; Sullivan, 1977; Jacobs and Noten, 1980). Indeed, it has been shown that the dissolved organic carbon (DOC) released by marine macrophytes (Penhale and Smith, 1977), although small, is assimilated by algal and bacterial populations associated with the macrophytes (McRoy and Goering, 1974; Brylinsky, 1977; Penhale and Thayer, 1980; Smith and Penhale, 1980). The low molecular weight (500-10,000 mw) fraction of DOC released from the leaves of three marine angiosperms (Thalassia testudinum, Zostera marina and Halodule wrightii) was differentially assimilated by bacteria in the periphyton of epiphytized plants whereas the high molecular weight (mw 10,00) fraction was not appreciably utilized (Wetzel and Penhale, 1979). Thus, release of DOC may enhance the growth of bacteria while converting dissolved carbon into particulate material that is subsequently incorporated into the marine food web by grazing organisms (Smith and Penhale, 1980).

Nutrient uptake by the roots of seagrasses and subsequent release of these nutrients via the leaves (McRoy and Barsdate, 1970; McRoy et al., 1972) bathe the periphyton in a nutrient-rich medium. Although net transfer of phosphorus from the roots via the leaves to the epiphytes of Zostera marina is small, 15 to 100% of the released phosphorus was assimilated by the associated epiphytes (Penhale and Thayer, 1980). Similarly, epiphytes of Z. marina take up nitrogen released by the seagrass (McRoy and Goering, 1974) even though bluegreen algae in the periphyton community were shown to fix large amounts of nitrogen (Goering and Parker, 1972). Both processes may play an important role in nitrogen cycles of seagrass habitats. It appears that dense epiphyte communities can be indirectly maintained by the uptake of nutrients released from the seagrass leaves as postulated by several workers (Harlin, 1971; McRoy and Goering, 1974).

The overall response of the periphyton to various metabolic exudates of marine phanerogams is poorly understood. Individual diatom species exhibit a highly varied response to different nutrients (Lee et al., 1973; Saks et al., 1976). Biochemical interactions may be partially responsible for the observation that the pennate diatom Cocconeis scutellum is the sole pioneer species on Zostera marina, forming an unialgal mat over newly formed blades (Sieburth and Thomas, 1973). The mat is in turn colonized by a variety of micro-organisms, primarily bacteria and other species of diatoms, all of which are incorporated in a thick mucous matrix (Fig. 1) (Sieburth and Thomas, 1973; van Montfrans et al., in press). The periphyton barrier slows

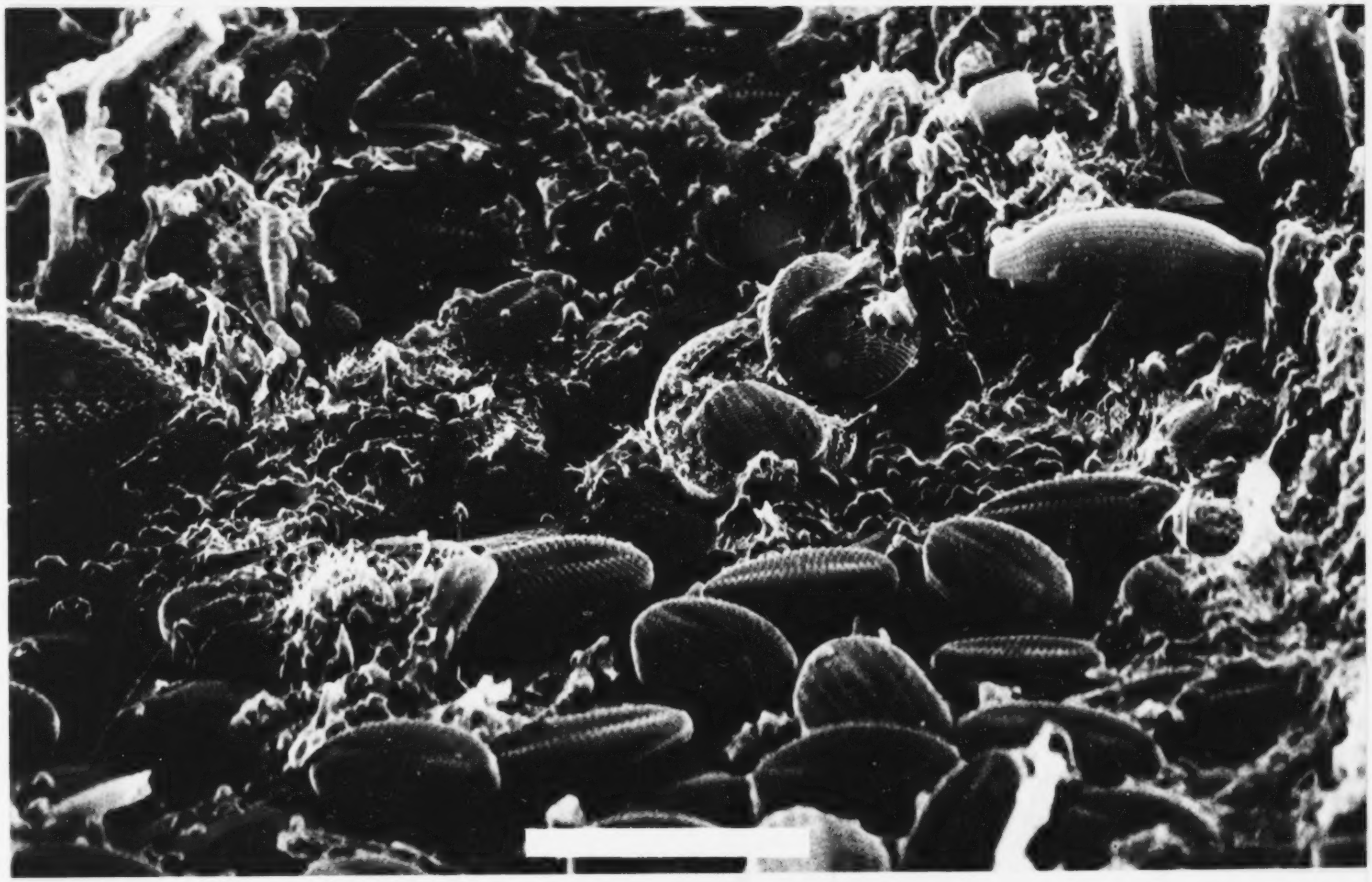

Figure 1. Scanning electron micrograph of the periphyton crust showing the diatom *Cocconeis scutellum* and bacteria adhering directly to the *Zostera marina* epithelium. Other pennate diatoms, blue-green algae, bacteria, and organic debris can be seen in the upper portions of the crust (440X; size bar = 10 μm) (from van Montfrans et al., 1982).

the diffusion of chemicals and nutrients into the surrounding water. Detritus (up to 80% volume, Kita and Harada, 1962) becomes incorporated in the mucous matrix as the periphyton community develops. It originates from the abundant epifauna associated with *Z. marina* (Marsh, 1973) although much of it also settles from the water column. This material further increases the surface area available for bacterial colonization and adds to the biochemical complexity of the periphyton crust. Although numerous abiotic factors including salinity, temperature, pH (Brown, 1962; Lee et al., 1975a, b), insolation (Main and McIntire, 1974; Borum and Wium-Andersen, 1980; Jacobs and Noten, 1980), nutrients released from the surrounding sediments (Reyes-Vasquez, 1970) and various environmental factors associated with tide levels (Penhale, 1977) affect the microcommunity, biochemical interactions between the seagrass substrate and the periphyton should not be overlooked.

c. Factors Which Reduce Fouling

Numerous factors reduce fouling on seagrasses. Some are strictly size related, whereas others involve complex biochemical mechanisms and growth responses evolved by the seagrass host. Ingestion of the periphyton crust on grass blades by the numerous grazers present in seagrass habitats also reduces fouling.

Macroalgae are restricted in their ability to successfully colonize submerged angiosperms by the size and nature of their attachment organ or basal disc (den Hartog, 1972). Algae with smaller basal discs are therefore able to colonize a greater variety of macrophytes than those with larger discs. It stands to reason that the broader leaved genera of marine vascular plants such as *Zostera* and *Posidonia* have a greater diversity of associated macroepiphytes than narrow leaved genera like *Ruppia* and *Syringodium*. May et al. (1978) found a greater diversity of epiphytes on *Posidonia australis*, a larger plant with a larger leaf area, than on *Zostera capricorni* and *Z. tasmanica* with less leaf surface area. Wood (1959) states that narrow leaved *Ruppia* had few epiphytes in a study of Australian macrophytes.

Like macroscopic algae, diatoms appear to be specific in their selection of a suitable sized substrate. Species such as *Cocconeis scutellum* which have a large surface area for attachment were shown to avoid finely branched algal thalli in preference for more thickly branched species (Ramm, 1977). It is possible that similar preferences exist for seagrasses with genera such as *Posidonia* and *Zostera* housing a greater complement of diatom species having a large attachment site than narrow bladed seagrass genera such as *Ruppia* and *Syringodium*. The genus *Cocconeis* is dominant on *Zostera marina* (Sieburth and Thomas, 1973; Jacobs and Noten, 1980) and *Thalassia testudinum* (Reyes-Vasquez, 1970; DeFelice and Lynts, 1978) whereas *Navicula povillardi*, a narrow diatom, accounted for one of every three individuals encountered on *Ruppia maritima* (Sullivan, 1977). Howard-Williams and Liptrot (1980) reported that *Zostera capensis* supported a considerably greater biomass of diatoms per unit mass of host tissue than *Ruppia cirrhosa* did in South Africa estuaries.

Macroalgae can also be excluded from successively colonizing marine phanerogams by the ephemeral nature of the macrophyte substrate. It is known that epiphytes of ephemeral nature are rare whereas perennial algae have a much greater association of macroepiphytes (den Hartog, 1972). A successfully colonizing epiphyte species must complete its life cycle according to a time scale that corresponds to the presence of the seagrass substrate. Similarly, Jacobs and Noten (1980) stressed the importance of seasonal growth patterns of *Z. marina* in determining community structural differences of the periphyton. They pointed out that seasonal growth ultimately regulated the average life time of the seagrass substrate and this in turn had an influence on epiphyton community structure.

Many seagrasses are known to rapidly produce new photosynthetic tissue. *Zostera marina* in Danish waters produced a new leaf every 14 days which had an average life span of 56 days (Sand-Jensen, 1977). Jacobs and Noten (1980) indicated that shoots of *Z. marina* along the coast of France produced a new leaf every 13 days in May when insolation was at a maximum and every 28 days in December when insolation was lowest. The average leaf turnover time for these months was 67 and 140 days, respectively. Rapid leaf growth ($\bar{x}$ = 1.22 cm per day) of the seagrass *Enhalus acoroides* was thought to enhance overall photosynthetic activity in this species (Johnstone, 1979). The photosynthetically useful life of *E. acoroides* blades was determined to be less than 25 days because of excessive fouling. Thus, it appears that the rapid production of new photosynthetic tissue had evolved in numerous seagrass species as a means of counteracting epiphytic loading (Sand-Jensen, 1977; Johnstone, 1979).

Seagrasses, in addition to evolving a rapid growth strategy to combat fouling, have also evolved chemical defenses. Phenolic substances which frequently act as growth inhibitors are found in a number of seagrasses (Zapata and McMillan, 1979). Although leaf extracts of *Posidonia oceanica* were found to stimulate the growth of the bacterium *Staphylococcus aureus* (Cariello and Zanetti, 1979), Harrison and Chan (1980) demonstrated growth inhibitory and lethal effects of extracts from recently dead (a few days to 2 weeks) *Zostera marina* leaves on microalgae and bacteria. These effects were inversely related to the age of the *Z. marina* leaves and at 35 and 90 days, antibacterial and antialgal activity, respectively, was completely lost. Phenols could determine the composition of the periphyton community by excluding some species of microalgae and bacteria and inhibiting the growth of others (Harrison and Chan, 1980). Their effects may be greater on the periphyton and encrusting algae than erect macroalgae because of the intimate association of the former two groups with the leaf surface. Although to our knowledge phenolic substances from seagrasses have not been demonstrated to be lethal or inhibitory to macroalgae, it would not be surprising to find that some algal sporelings are adversely affected by these compounds.

Biological interactions between epiphytes and grazers can have a great impact on the structure and function of both macroalgal and periphyton associations. Studies on macroalgae colonizing inert substrates have shown that grazers have a dramatic effect on biomass and species composition of macroalgal assemblages (Southward, 1964; Kain and Svedsen, 1969; Dayton, 1971; Lein, 1980). Herbivore-plant interactions involving microalgal communities indicate that grazing mollusks can drastically reduce the biomass of intertidal epilithic diatoms (Castenholz, 1961). Some periphyton grazers maintain community dominance by tightly adhering diatoms by removing the outer, loosely adhering portions of the diatom mat (Nicotri, 1977) and others feed on a mixed diet of two encrusting algal species in a fixed proportion even over a wide range of availability of the two foods (Kitting, 1980). Few studies have elucidated the role of epiphyte grazing in seagrass habitats. These interactions will be discussed more thoroughly in a later section.

d. Implications of Epiphytism for the Seagrass Host

Both beneficial and adverse effects of epiphytes on macrophytes have been mentioned in the scientific literature. Most are based primarily on observational information, however, and quantitative data are generally lacking.

Algal mats are frequently found associated with grass beds in some parts of the world. These mats, while still attached to seagrasses, are formed by intertwined algal filaments and create a canopy over the grass bed. They can have a profound affect on the associated community (Wood, 1972) under conditions of minimal water circulation. Due to increased photosynthesis by the algae, the ambient pH level rises to 9.4 in extreme cases. The bicarbonate ion becomes limiting at such a high pH and photosynthesis ceases. A drop in pH to less than 7.0 occurs during night time respiration with a concurrent drop in the redox potential to negative values. Mortality of some animals occurs and the growth of many plants is limited due to such fluctuations (Wood, 1972). Algal mats have been shown to have a limiting effect on the growth of *Ruppia maritima* and observed to cause temperature stratification in the water column due to shading (Richardson, 1980). Such stratification can postpone flowering, fruiting and seed production in *R. maritima*. If shading by algal mats is severe, active photosynthesis is restricted to the upper layer of the water column. As a result of thermal stratification also due to shading, the photosynthetically oxygenated water does not reach the lower portions of the water column. Because of the high oxygen demand of the benthos, and night time plant respiration, anaerobiasis occurs below the upper stratum (Richardson, 1980) in a manner similar to that reported by Wood (1972). Grass beds exhibiting such extreme characteristics are associated with environments having little water circulation. The instability of conditions associated with such systems results in generally depressed levels of abundance and diversity of the associated fauna. When the macroalgal mats detach from the host plants and float off of the grass beds, stressful conditions are alleviated and resistant plants and animals are once again able to flourish.

Algal epiphytes can have more subtle yet equally important effects on marine phanerogams. Breakage of leaf tips, heavily encrusted by calcareous algal epiphytes, has been reported to occur in *Thalassia testudinum*. This is primarily caused by leaf decay beneath epiphytes and is a characteristic feature of *T. testudinum* beds at Barbados (Patriquin, 1972). Similar encrustations occur on *T. testudinum* in Florida Bay (Ginsburg and Lowenstam, 1958; Humm, 1964) and serpulid worms, in addition to calcareous algae, are commonly found in Jamaica growing on the blades of *T. testudinum* (Land, 1970). Both calcareous red algae (generally melobesoids) and serpullid worms have a similar detrimental effect on the macrophyte host as that reported by Patriquin (1972). Upon death, these carbonate-secreting organisms can contribute significantly to the carbonate sediments of *T. testudinum* beds (Land, 1970; Patriquin, 1972). The depositional environments of grass beds is well documented (Daetwyler and Kidwell, 1959; Guilcher, 1965; Scoffin, 1970; Burrell and Schubel, 1977) and a portion of this phenomenon is directly attributable to the presence of a multitude of epiphytes which not only produce carbonate sediments upon their death but also trap fine suspended sediments that are subsequently added to those of the grass bed (Ginsbur and Lowenstam, 1958; Swinchatt, 1965; Scoffin, 1970; Taylor and Lewis, 1970).

More severe effects of epiphyte fouling are attributed to shading of the macrophyte host. In New Guinea, fouling of *Enhalus acoroides* by epiflora and epifauna occurs rapidly and new growth of leaf tissue is no longer visible through the mass of colonists after only 10, and occasionally up to 25, days (Johnstone, 1979). Such shading can severely reduce the amount of light whch reaches the host. Taylor and Lewis (1970) studied six species of marine angiosperms of the Seychelles Archipelago and reported that "there is often such a thick coating of epiphytes on the grass leaves that they appear to be covered by a thick brown fur. They render so much of the photosynthetic surface of the plants non-functional that the growth of the angiosperms must be affected." Borum and Wium-Andersen (1980) determined that epiphyte biomass increased exponentially from the youngest leaf of *Z. marina* to the oldest leaf and that on any single blade a similar increase occurred from the basal (or youngest) portion to the tip or oldest part of the blade. Furthermore, they demonstrated that less than 10% of the incoming light was transmitted through the dense epiphyte cover growing on the oldest blade tips of *Zostera marina*. In contrast, more than 90% of the ambient light was available for photosynthesis to the lightly epiphytized basal portions of the blades. Since the wavelength of light absorbed by the periphyton growing on *Z. marina* is virtually identical to that utilized by the host (Fig. 2), the amount of usable light reaching the *Z. marina* blade can be severely reduced by periphyton fouling (Caine, 1980).

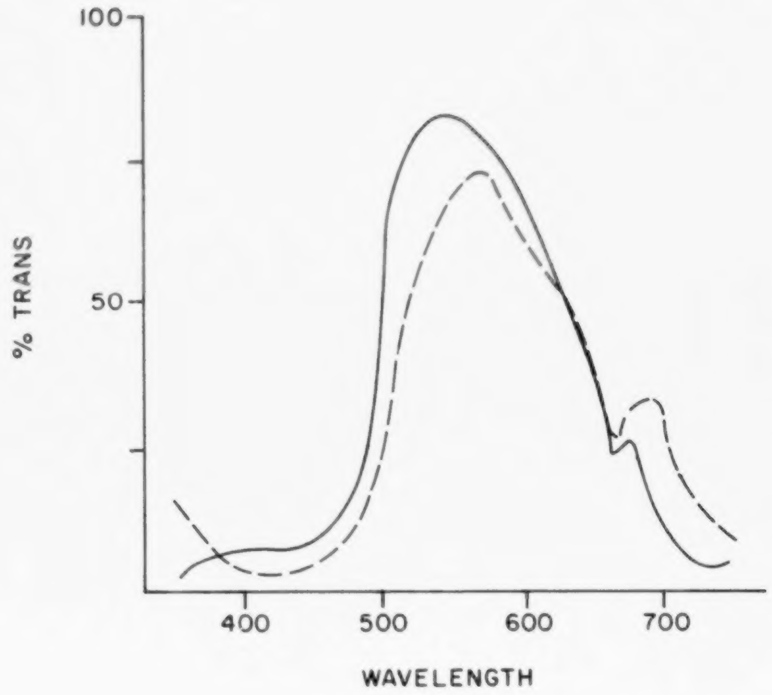

Figure 2. Light transmittance of methanol extracted pigments of Zostera marina (------) and of periphyton (------) growing on Z. marina blades. The similarity of the curves indicates that both periphyton and Z. marina use similar light wavelengths and that periphyton reduces the amount of usable light reaching the Z. marina blade (from Caine, 1980).

The effects of epiphytes on eelgrass (Zostera marina) photosynthesis has been further documented by Sand-Jensen (1977). He found that diatoms, primarily Cocconeis scutellum, formed a crust over the leaves of Z. marina and considerably reduced photosynthesis by both limiting the available light and acting as a barrier to carbon uptake. Photosynthesis was reduced 31% by epiphytes under optimal light conditions and ambient (about 1.7 $\mathrm{meg \cdot l^{-1}}$) HCO_3^- concentrations (Fig. 3). Beer et al. (1977) demonstrated that HCO_3^- is the major carbon source for photosynthesis in seagrasses and that uptake occurs readily across the leaf surface. The diffusion of HCO_3^- was depressed by the epiphyte crust causing reduced photosynthesis (Fig. 4) at varying HCO_3^- concentrations and a constant light intensity of 14.7 $\mathrm{mW \cdot cm^{-2}}$ (Sand-Jensen, 1977). Light attenuation experiments using shades have confirmed the impact of reduced light on seagrass growth. Backman and Barilotti (1976) reduced downwelling illumination over Zostera marina by 63% and found a significant reduction in numbers of both vegetative and flowering shoots. Similar shading experiments have shown that production of Ruppia maritima is substantially reduced by decreased illumination. Light reductions of 80% or more for 100 days completely precluded R. maritima and light reductions of 20% for 250 days significantly decreased its biomass (Congdon and McComb, 1979). Heavy epiphytic loading was attributed to the cause for earlier dieback and lower production estimates in one Ruppia cirrhosa bed than that found for an adjacent epiphyte free stand of R. cirrhosa (Kiørbe, 1980a). Furthermore, it is thought that light most likely controls the lower depth distribution of marine macrophytes (Burkholder and Doheny, 1968; Phillips, 1972; Thayer et al. 1975; Jacobs, 1979; Mukai et al. 1980). Since epiphytes diminish the amount of light reaching the macrophyte, they may partially and indirectly influence plant distribution, biomass, productivity, and both asexual and sexual reproductive capability.

II. THE TROPHIC ROLE OF PERIPHYTON IN SEAGRASS BEDS

It is well known that the direct consumption of seagrasses by marine organisms is minimal (<5% of the total production) and that most of the carbon fixed by marine angiosperms is transferred to higher trophic levels via a detrital pathway (Fenchel, 1977; Klug, 1980; and references contained therein). However, some macrophyte carbon can be transferred indirectly through the ingestion of periphyton which, as discussed earlier, assimilates some of its carbon from DOC released by the host macrophyte (Thayer et al., 1978). Furthermore, the highly productive diatom and bacterial component of the periphyton is responsible for a considerable percentage of the production of grass bed ecosystems. On a per unit area basis, epiphytes contribute an average of from 18% (Penhale, 1977) to 50% (Borum and Wium-Andersen, 1980) of the combined Zostera marina leaf and epiphyte production and 22% of the production in a Thalassia testudinum bed (Jones, 1969). This production is available for consumption by the numerous grazers found in seagrass habitats.

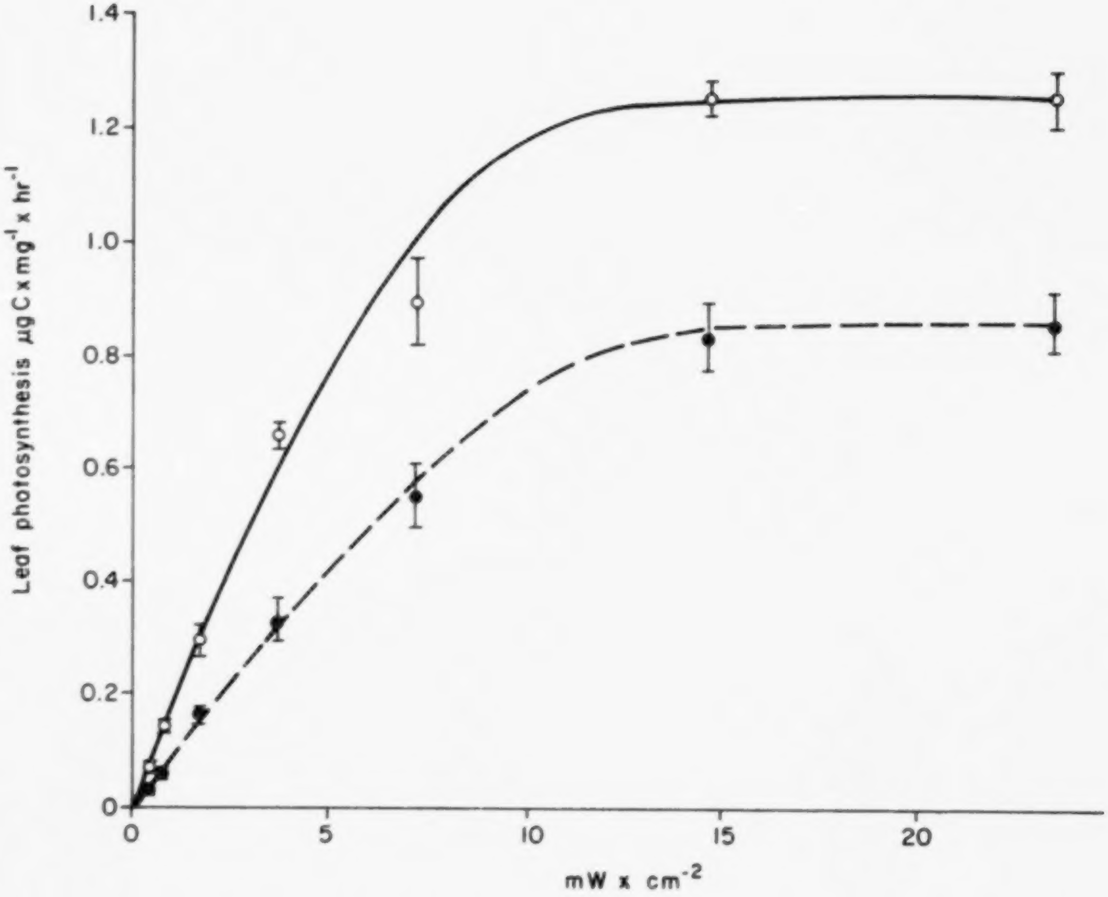

Figure 3. The photosynthesis of the third leaf of Zostera marina with epiphytes (·, broken line) and without epiphytes (o, solid line) as a function of light intensity. Each value represents the mean (± SE) of four samples (from Sand-Jensen, 1977).

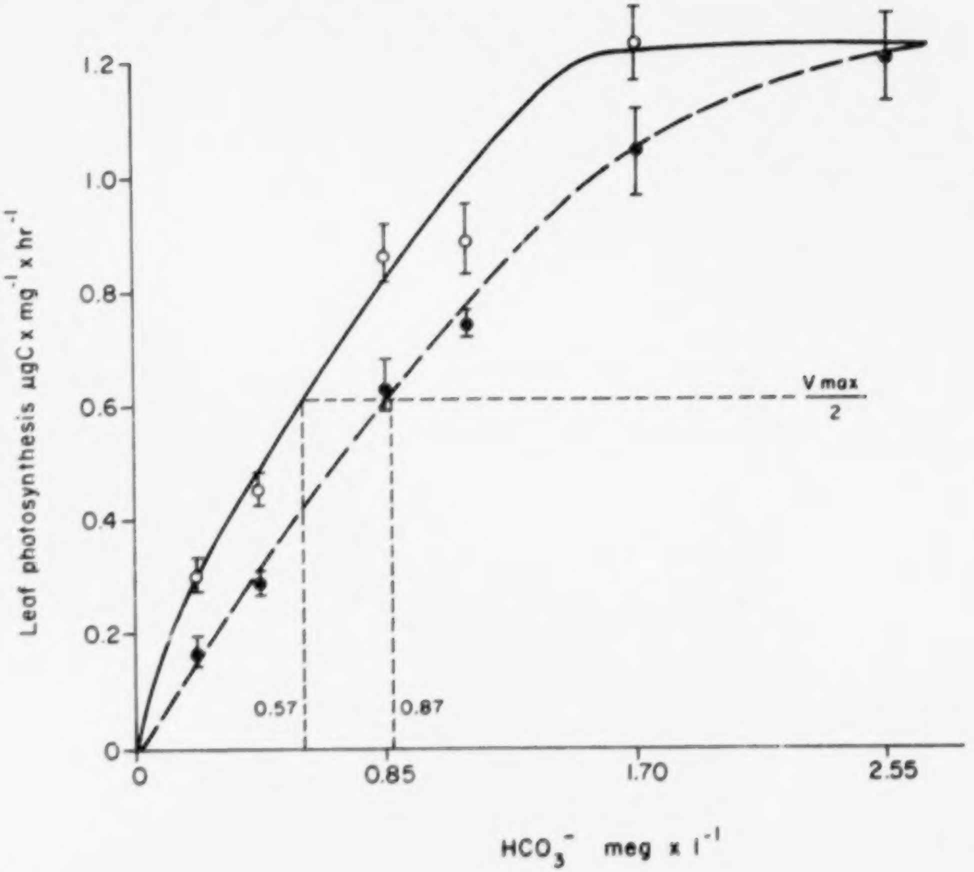

Figure 4. The photosynthesis of the third leaf of Zostera marina with epiphytes (•, broken line) and without epiphytes (o, solid line) as a function of HCO_3^- concentration. Each value represents the mean (± SE) of four samples. The half saturation constants (K_z) of the two curves are given. Light intensity, 14.7 mWcm^{-2} (from Sand-Jensen, 1977).

Although the productivity of the periphyton in seagrass habitats appears to be substantial, few quantitative data on the utilization and importance of this food resource are available. For limnetic environments, the trophic importance and ecological relationships of the periphyton are somewhat better understood (see Hutchinson, 1975, for review). Brook (1952, 1955) brought to light the substantial impact of grazers on aquatic filamentous algae and diatoms growing both on inert substrates and macrophytes of freshwater systems. The nutritional value of periphyton based on carbon to nitrogen ratios was substantially higher than that of freshwater macrophytes. In marine and estuarine habitats, studies on the trophic dynamics of the meiofauna indicated that diatoms in a salt marsh aufwuchs (= periphyton) community were important food for numerous protozoans (Lee et al., 1966; Lipps and Valentine, 1970; Lee et al., 1975a, b). Certain species of diatoms, chlorophytes and bacteria constituted the bulk of material eaten by foraminiferans and could apparently be selectively grazed from among numerous other species present in the periphyton (Lee et al., 1973). Some species such as the harpacticoid copepod *Nitocra typica* feed on periphyton and were shown to have very complex nutritional requirements depending on and influencing *N. typica*'s different life cycle stages (Lee et al., 1976). Similar importance of diatoms and bacteria in the feeding behavior of marine nematodes was demonstrated by Tietjen and Lee (1977). Comparable studies in seagrass habitats are limited although the nutritional role of the periphyton is probably similar.

Numerous authors mention the importance of the periphyton as a food source to resident consumers in grass beds (Wood, 1959; Marsh, 1973; Brasier, 1975; Kikuchi and Perez, 1977; Harlin, 1980; Ogden, 1980). One of the dominant groups of the epifaunal community in many vegetated habitats are gastropod mollusks (Marsh, 1973). Taylor and Lewis (1970) estimated that the prosobranch molluscan fauna associated with a *Thalassia hemprichii* bed is primarily epifaunal and, of these, approximately 30% were composed of algal feeders which rely primarily on the microepiphytes that coat the blades of *T. hemprichii*. However, no quantitative data were presented to support their contention. Kikuchi and Perez (1977) mentioned that the primary dietary component of the sea hare, *Aplysia* sp., was the epiphytic algae associated with seagrass blades. Stomach content analyses of the large and economically important tropical gastropod *Strombus gigas* revealed that this species also relied primarily on epiphytic algae found growing on the blades of *Thalassia testudinum* although it also ingested algae and some macrophyte tissue (Randall, 1964). A similar role in *T. testudinum* and *Halodule wrightii* beds is played by the small prosobranch *Modulus modulus* which is commonly encountered in tropical Atlantic vegetated habitats. *M. modulus* feeds primarily on epiphytic algae and accumulated detritus of marine macrophytes and, through its grazing activity, it may also dislodge newly settled larvae of other epifaunal organisms thereby reducing the overall fouling on grass blades (Mook, 1977). *Bittium varium*, the small, dominant epifaunal gastropod of Chesapeake Bay *Zostera marina* beds (Marsh, 1976), can reduce periphyton weight (g·dry wt per cm^2) on polypropylene ribbon resembling *Z. marina* by a factor of almost 63% (van Montfrans et al., in press). Scanning electron micrographs of *B. varium* feeding trails revealed that in some instances removal of the periphyton crust was complete (Fig. 5), although in other cases feeding appeared to be mechanically selective for the upper layers of the periphyton crust leaving behind the loosely attached bacteria which were too small to be removed and the more tightly adhering diatom *Cocconeis scutellum* (Fig. 6). The importance of diatoms in the diet of both *Bittium alternatum*, a sympatric congener of *B. varium* in the Chesapeake Bay, and the mud snail *Nassarius obsoletus* was illustrated by Lee et al. (1975c) who showed that together these snails ingest about 10^7 algal cells per day. Another species of gastropod, *Littorina saxatalis*, is abundant in *Z. marina* meadows along the coast of Nova Scotia. This species was found to inhabit live vegetation during the warmer months from March to November and to rely primarily on periphyton as its food source (Robertson, 1981). The population dynamics of *L. saxatalis* were closely linked to the limited food supply (i.e. periphyton) growing on *Z. marina* leaves and intraspecific competition for this resource was shown to be responsible for post recruitment mortalities.

The role of micro- and macroepiphytes in the trophic dynamics of crustaceans has also been demonstrated to a limited degree. Brawley and Adey (1981) showed that amphipod grazing had a substantial effect on the biomass of microalgae in a coral reef microcosm. They also demonstrated the effect of grazing in changing the community structure of algal species present. Amphipods are a particularly diverse component of seagrass habitats (Marsh, 1973; Nelson, 1980). As a group they exhibit varied feeding habits including both macrophagy and microphagy of algae associated with the macrophytes and seagrass detritus (Zimmerman et al., 1977). Resource partitioning studies of four amphipods species inhabiting *Thalassia testudinum* and *Halodule wrightii* beds in the Indian River region of Florida showed that between 29 and 66% of the food ingested by all four species was composed of microepiphytes and between 2 and 35% was made up of macroalgae (Zimmerman et al., 1979). High assimilation efficiencies of carbon-14 labeled microalgae further emphasized the relative importance of microepiphytes in the diet of these amphipods. The importance of microalgae in the diet of the caprellid amphipod, *Caprella laeviuscula*, was illustrated by Caine (1980). This species scrapes periphyton from the blades of *Z. marina* (Caine, 1979). Laboratory grazing experiments have shown that control blades of *Z. marina* without *Caprella laeviuscula* had over four times the periphyton biomass than those upon which *C. laeviuscula* was allowed to graze (Caine, 1980). Although no nutritional data were presented, *C. laeviuscula* appears to depend heavily on the presence of periphyton as a food source. A decapod crustacean, *Palaemonetes pugio*, was shown to voraciously consume epiphytes attached to *Halodule wrightii* rather than the grass itself (Morgan, 1980). Epiphytes constituted an important part of the diet in *P. pugio* although larger shrimp (>19 mm) preferred mysids as a food source when present. Microepiphytes were assimilated at rather high mean efficiencies of 83% by *P. pugio*. Species of *Palaemonetes* are among the most numerous components of the

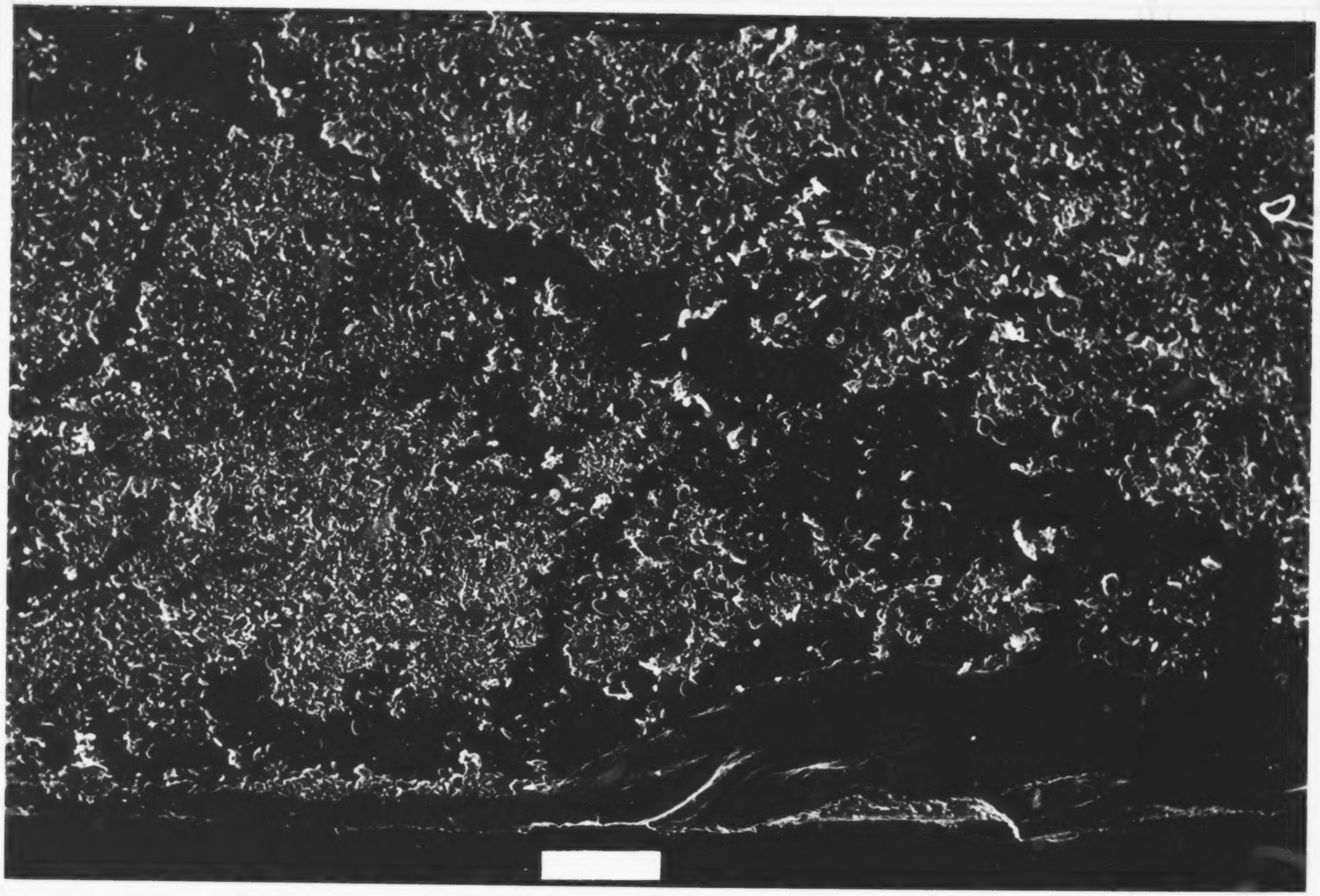

Figure 5. Scanning electron micrograph of *Bittium varium* feeding trails on *Zostera marina* showing complete removal of the periphyton crust where grazing occurred (200X; size bar = 100 μm) (from van Montfrans et al., 1982).

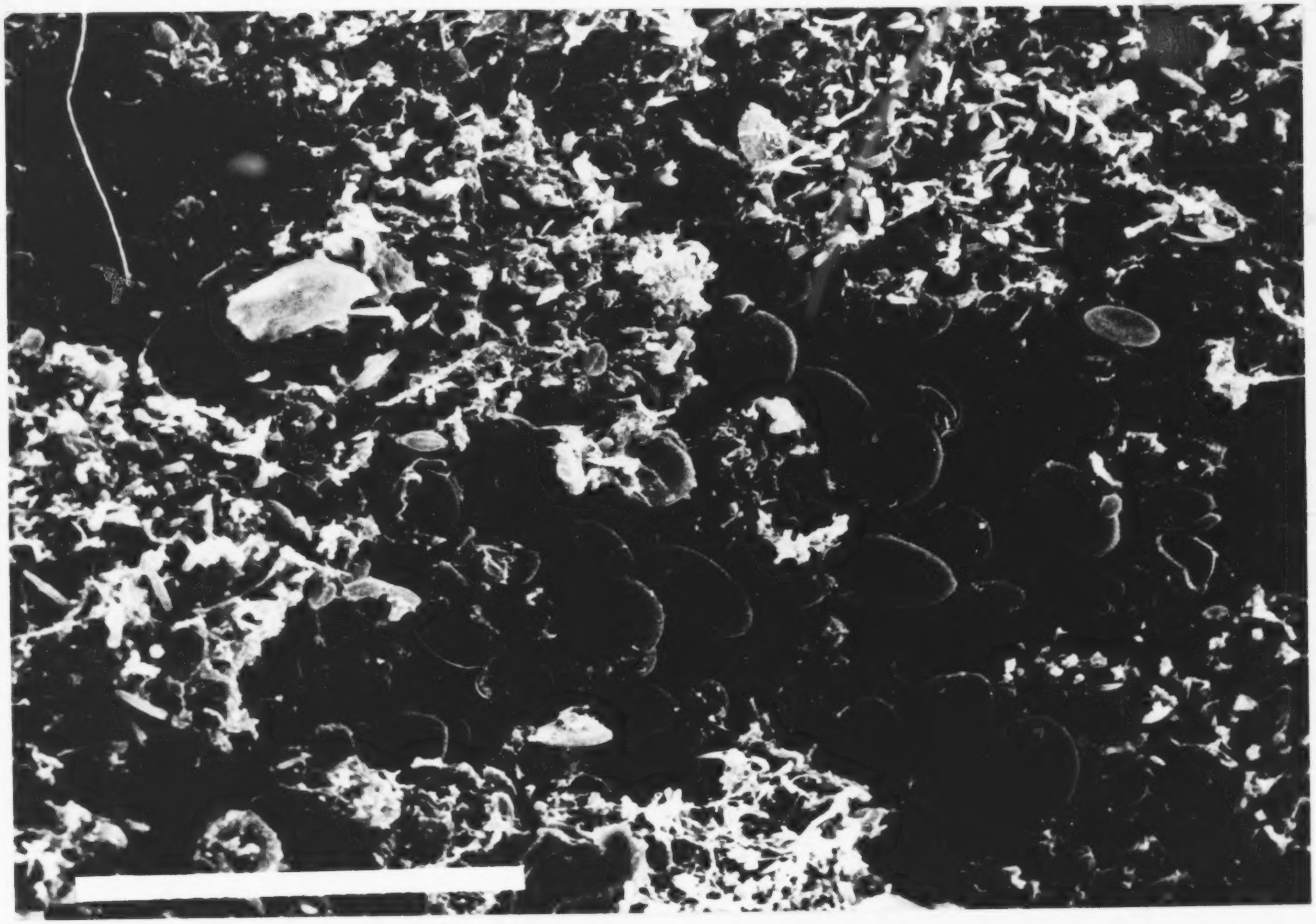

Figure 6. Scanning electron micrograph of a grazed patch on *Zostera marina* showing the removal of the upper half of the periphyton crust. The majority of the slender pennate diatoms (*Amphora* and *Nitzschia*) in the upper portion of the crust were consumed. The diatom *Cocconeis scutellum*, which adheres tightly to the epithelium, has the lower half of the frustule still attached. Additional damage to several *C. scutellum* is evident as cracks or holes in the frustules (300X; size bar = 100 µm) (from van Montfrans et al., 1982).

vagile epifauna in seagrass beds of the northeastern U.S. coast (Heck and Orth, 1980). These species and ecological equivalents in other parts of the world could play a role similar to that of P. pugio in other seagrass habitats.

A third major group of organisms which occur epifaunally on seagrasses are polychaetes. Because of their generally high fecundity, polychaetes exhibit seasonal pulses of abundances in temperate and cold water areas. Little is known about their diets, however, although a recent interest in polychaete feeding habits is evident in the literature (Fauchald and Jumars, 1979). To our knowledge, there is no information on the utilization of seagrass periphyton by polychaetes. It seems likely, however, that species which exhibit a surface deposit feeding mode could ingest some periphyton.

Some fish have been shown to directly ingest microscopic algae (Hiatt, 1944; Wood, 1959; Bell et al., 1978). A detailed study of leather jackets (Class: Pisces, Family: Monacanthidae) in an Australian estuary showed that although large amounts of seagrasses were ingested, the fish were highly dependent on the encrusting fauna and epiphytic algae for their nutrition (Bell et al., 1978). Wood (1959) further emphasized the role of direct grazing on epiphytes by phytophagous fish and suggested that seasonal variation in the weight of epiphytes on Zostera capricorni might partially be influenced by the extent of fish movements and seasonal food preferences.

The exact amount of periphyton carbon produced by and later removed from grass bed habitats is poorly understood but it appears that it is an important component of energy flow patterns in seagrass ecosystems. The trophic importance of mollusks, crustaceans and polychaetes is well established in the literature although a thorough review is beyond the scope of this paper. It is generally thought that predation, which can be mediated by grass density, is an important structuring force in determining the composition of the epifaunal community associated with seagrasses (Kikuchi, 1974; Young and Young, 1978; Conacher et al., 1979; Nelson, 1979a, b; Stoner, 1979, 1980; Wilkins, pers. comm.). By feeding heavily on epifaunal organisms, many of which are periphyton grazers, predators such as fish, crabs, and birds cycle carbon fixed by the periphyton to higher trophic levels. Trophic relationships in a west Florida mixed bed of vegetation indicated that peracaridan crustaceans and polychaetes were the main sources for energy transferred from primary consumer levels to higher trophic levels (Carr and Adams, 1973). Similar trophic links were found in a southeastern Florida Thalasia testudinum bed (Brook, 1977) and based on a study of the feeding ecology of a Zostera marina fish community, 56% of the diet by weight of food items such as eelgrass, crustaceans, gastropods, and detritus originated in grass beds (Adams, 1976).

Benthic pelagic coupling was demonstrated during a study of seagrass habitats in Australia. Robertson and Howard (1978) found that benthic amphipods and ostracods exhibited vertical migration into the water column at night and were therefore actually facultative zooplankters. These amphipods and ostracods were heavily preyed upon by midwater planktivorous fish when nocturnal switching in prey selection occurred in response to the abundance of facultative zooplankters. Thus, numerous invertebrates in grass beds, many of which are grazers, provide links with species in higher trophic levels.

III. PERIPHYTON GRAZING: CONSEQUENCES FOR THE MACROPHYTE HOST

The secondary effects of periphyton grazing in energy flow and nutrient cycling patterns of vegetated habitats is virtually unknown. Obviously, much of the material ingested by periphyton grazers enhances detrital pathways and recycles nutrients through the production of feces. A more subtle consequence of grazing, however, may be seen in the macrophyte host's response to the removal of the periphyton crust. Few studies have addressed this concept with a quantitative approach although several inferences can be made from published literature regarding the positive effects of such grazing activities.

During an extensive study of *Ruppia maritima* in New Hampshire tidal marshes, Richardson (1980) observed that, "numerous small snails of the genus *Hydrobia* were seen grazing the epibiota present on *Ruppia* plants under the algal mats to the extent that the plants were nearly free of epibiota throughout most of the season." These plants were considered to be healthy and vigorous. Mook (1977) observed reduced fouling of tiles due to the grazing activities of *Modulus modulus*, a gastropod which is common in tropical Atlantic grass beds. He suggested that the presence of the snail minimizes fouling on seagrass blades although he did not emphasize the significance of such activity in terms of host plant responses. Similarly, Robertson (1981) showed by grazer exclusion experiments that the snail *Littorina saxatilis* controlled the amount of periphyton on *Zostera marina* leaves. Several authors have discussed the implications of grazing on periphyton for the macrophyte host by removing this barrier to light. van Montfrans et al. (in press) suggested that loss of the dominant periphyton grazer, *Bittium varium*, a prosobranch gastropod, from *Zostera marina* beds in the Chesapeake Bay, USA, may have had important implications for the recent decline of *Z. marina* in the Bay (Orth and Moore, 1981a, b). Caine (1980) stated that the presence of the caprellid amphipod *Caprella laeviuscula* "allowed *Z. marina* to grow in areas where it would otherwise have been excluded by periphyton." In experimental tanks with the seagrass *Heterozostera tasmanica*, Howard (in press) showed that the presence of gammaridean amphipods had a significant impact on epiphytic fouling compared to tanks without the amphipods. He suggested that the secondary effects of grazing ultimately influenced macrophyte productivity and energy flow pathways in seagrass habitats. We have further experimental evidence that transplanted plugs of *Z. marina* produced a significantly greater number of new shoots, had a greater leaf biomass and leaf area index and were less fouled by periphyton when the grazer _B. varium_ was present than did control plugs in the absence of grazers (unpublished data). Thus, it seems very likely that periphyton grazers, when present, can have a substantial, though indirect, impact on the proliferation, biomass and reproductive potential and, possibly, the persistence of seagrasses.

We recommend that researchers be critically aware of the indirect influence of periphyton grazers on seagrass productivity. Comparisons of productivity measurements between both local grass beds and those separated latitudinally must consider biological interactions that influence primary production as well as abiotic variables. Reported causes for spatial and temporal differences in seagrass productivity due to insolation, temperature, and nutrients may be only partially valid if those systems harbor dense assemblages of periphyton grazers.

We have developed a very simplified model that attempts to place the role of periphyton grazers into their functional perspective. We have generated a series of hypotheses based on this model that will ultimately have predictive value when considering the effect of increased fouling on seagrass productivity and the role that periphyton grazers play in influencing this relationship.

In our model we assume that species of seagrasses occur from very shallow water where light is never limiting to deeper areas where light levels are so low that phanerogams are only minimally sustained. Under these conditions there will generally be a decrease in seagrass productivity as periphyton production (i.e. fouling) increases. Seagrass production relative to the degree of epiphytic fouling may vary somewhat with depth (i.e. light).

Under light saturated conditions and when photoinhibition does not occur, seagrass production varies with the degree of epiphytic fouling as depicted in Fig. 7. Initially, seagrass production would be minimally affected by fouling since the plants receive adequate light to achieve high primary production. However, as epiphytic fouling increases, seagrass productivity declines more rapidly because of diminished light levels. Ultimately, fouling would cause net seagrass productivity to be negative and the plants would die. The presence of grazers in this situation would shift the seagrass production curve to the right by removing the light barrier. Thus, at a particular level of epiphytic fouling (point a), the same seagrass habitat would exhibit higher levels of primary production when grazers are present (point b) than in the absence of grazers (point c). Conversely, two seagrass beds having the same level of primary productivity (points d and e) may be similar in this regard primarily because one experiences greater fouling (point a) than the other (point f). These relationships may be important in systems receiving moderate nutrient enrichment. Fouling by epiphytic algae in such systems would increase and without grazers to keep fouling in check, the macrophytes would experience death due to light reduction below the compensation point.

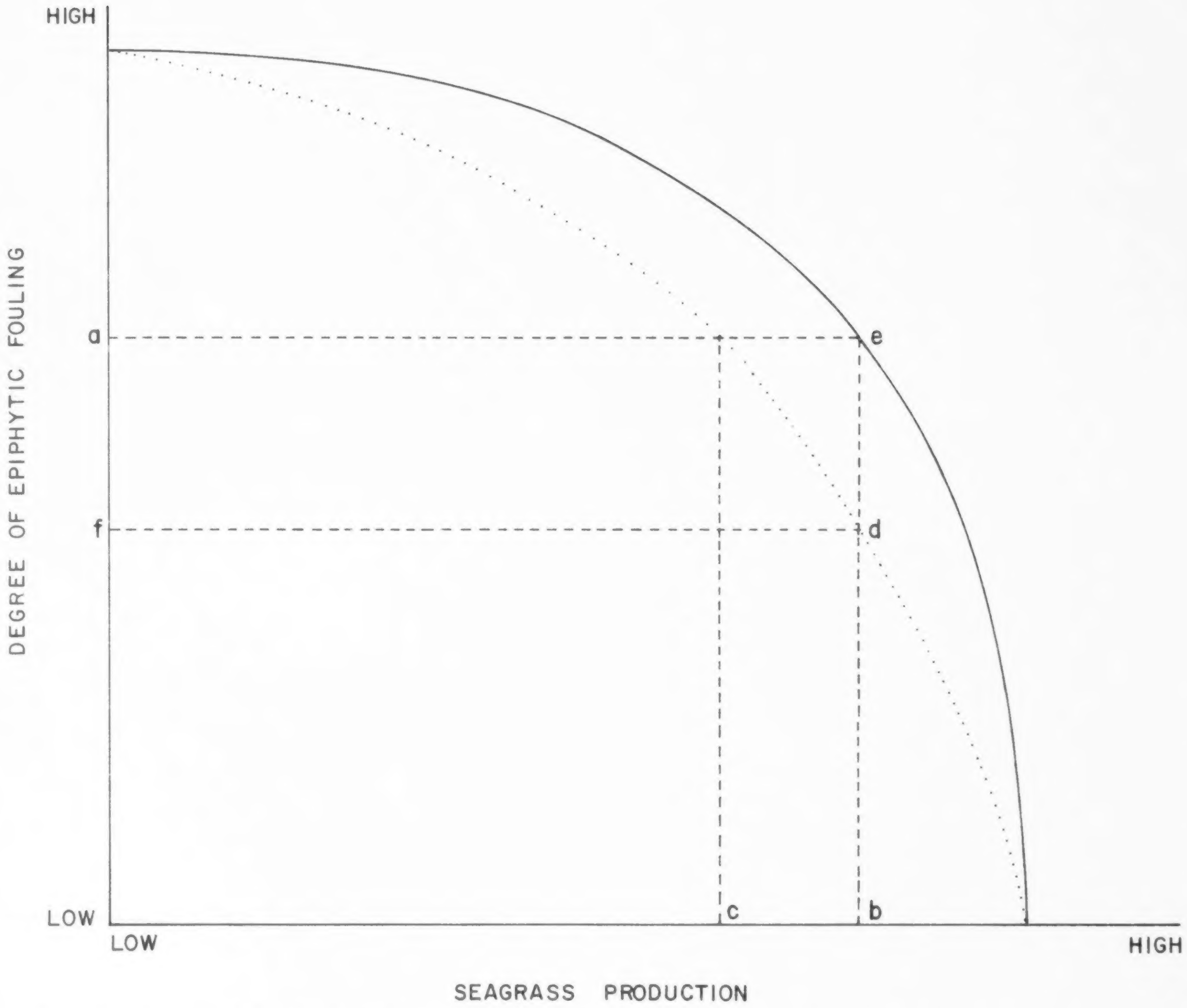

Figure 7. Hypothetical model of the effects of epiphytic fouling on seagrass production in the presence (------) and absence (......) of periphyton grazers. We make the assumption that light saturated conditions exist for maximal production in our model.

One aspect of seagrass-fouling relationships not depicted in our model concerns the beneficial effects of epiphyte cover under certain circumstances. Plants which grow in shallow water or are very sensitive to high light levels may be subject to photoinhibition. Some may also experience desiccation if exposed at low tide. In these situations, epiphytic fouling may actually be responsible for or at least enhance the productivity of the seagrass. Removal of this protective crust by grazing would result in reduced seagrass productivity due to photoinhibitory effects and also increase the susceptibility to desiccation. Of course, extremely dense growths of attached algae and fouling organisms would have similar effects as those already discussed.

We recognize that our hypothetical model represents an oversimplification of a complex system. Any number of factors, acting independently or synergistically, may affect seagrass productivity. The timing of epiphyte fouling in relation to seagrass production and/or life history stage, interference of chemical diffusion across the leaf surface caused by periphyton, the effects of light reduction due to phytoplankton and periphyton, the ability of a seagrass to rapidly regenerate new photosynthetic tissue and slough off epiphytized leaves, differences in light requirements of individual seagrass species, and the density of periphyton grazers, all either indirectly or directly affect seagrass productivity. However, the actual quantity and quality of light reaching the plant surface will be the ultimate factor affecting the survival of an established seagrass species. Therefore, periphyton grazers may represent a very important interactive element in affecting light penetration to the leaf surface in those areas where they are abundant.

Based on the relationships depicted in our model, we can make some predictions on the effect of environmental perturbations which diminish the light reaching the plant surface. Light reductions resulting from greater fouling, increased suspended particulates in the water column, or a reduction of periphyton grazers will cause a decline of seagrasses along a depth gradient with reductions occurring first in deepest areas and progressing inshore depending on the amount of light reduction. We also predict that the horizontal distribution of seagrasses along an estuarine turbidity gradient will shift away from areas of greatest turbidity. Furthermore, these shifts will not be as pronounced in seagrass systems with a large component of periphyton grazers.

IV. EFFECTS OF NUTRIENT ENRICHMENT ON MACROPHYTES

The nutrient composition of estuaries varies considerably from one system to another depending on numerous factors, including the type of estuary, the amount of freshwater discharge into the estuary, geological and geochemical characteristics of each drainage basin, storm events, biological uptake of nutrients and anthropogenic inputs (Briggs and Cronin, 1981). In most estuaries, nitrogen is commonly the most limiting nutrient (Nixon, 1981) and changes in nutrient composition from anthropogenic sources are known to have numerous effects. However, very little is known about the consequences of such changes on macrophyte distribution and abundance. The proceedings of a recent international symposium on the effects of nutrient enrichment in estuaries (Neilson and Cronin, eds., 1981) included 33 papers, none of which addressed the effects of eutrophication on submerged angiosperms. Limnologists have a better understanding of such effects and although the nutrient kinetics in estuaries may be more complex than in lakes, some insight into eutrophication-macrophyte relationships might be derived from examining the freshwater literature.

During a study of progressive nutrient enrichment in Norfolk Broads, a series of lakes in England, Phillips et al. (1978) formulated an hypothesis to explain the disappearance of dense macrophyte stands. It was postulated that epiphytic algae (mainly diatoms) were initially favored by the eutrophication process and responded by increased proliferation. As a consequence, macrophyte-epiphyte complexes ultimately declined and were replaced by phytoplankton populations. Thus, shading by epiphytes due to progressive eutrophication appeared to be the causative agent in macrophyte declines and phytoplankton increases were a subsequent development. This hypothesis was further substantiated by Moss (1979) whose study of two centuries of diatom records from the sediment in one of the lakes confirmed that epiphytic diatoms reached very high abundances over time and then began to disappear as fouling caused the demise of the host substrate. Subsequently, sediment cores showed an increase in planktonic diatoms which persisted to the present. This sequence of events might be predicted based on previous research. Hasler and Jones (1949) demonstrated that aquatic macrophytes had a growth inhibiting effect on microalgae (i.e. epiphytes and phytoplankton) but based on Fitzgerald's (1969) work this was shown to be the case only when nutrients were limiting. Fitzgerald (1969) demonstrated that under nutrient limited conditions the filamentous green algae *Cladophora* sp. remained relatively free of epiphytes but when surplus nitrogen was available, excessive epiphytic fouling occurred. Additional evidence from freshwater studies indicated that nutrient enrichment influences community composition of periphytic diatoms (Eminson and Moss, 1980). When nutrients in the external environment are limiting, macrophytes exert a chemical influence on colonizing diatoms causing a host specific relationship. Under more fertile conditions, host specificity breaks down and all periphytic communities are alike in composition. This is accomplished by favoring faster growing diatom species which, unlike slow growing diatoms, which are adapted for uptake of nutrients at low concentrations under infertile conditions (Moss, 1973; Eminson and Moss, 1980;), are more chemically dependent on open water for their nutrients (Eminson and Moss, 1980).

Similar relationships in estuaries have not been demonstrated although it is very likely that the periphyton community as well as plankton populations rather than macrophytes are favored by anthropogenic nutrients. Marine macrophytes derive most of their nutrition from the soil in which they grow and thus incorporation of nutrients into the sediments would be a prerequisite for enhanced macrophyte growth. Epiphytes and phytoplankton, on the other hand, respond more immediately to nutrient enrichment by dissolved nutrients. Consequences of such responses in estuaries would be the same as in freshwaters, ultimately reducing the light available to macrophytes thereby causing their demise.

Numerous studies in the marine environment have documented changes in macroalgal community composition due to eutrophication. Generally, increased nutrients disrupt the competitive balance between perennial algae such as fucoids and ephemeral green algae by favoring the latter (Bokn and Lein, 1978). Low production of macrophytes has been attributed to urbanization although the exact mechanism for this phenomenon was not discussed (West and Larkum, 1979). Macroalgae epiphytic on Zostera marina were favored by eutrophication which caused an increase in both the growth and numbers of individuals on the host plants (Larkum, 1976). These responses were shown to ultimately cause the disappearance of the grass beds in the polluted portion of the estuary. Larkum (1976) also pointed out that once degeneration of seagrasses is begun, the processes become autocatylitic as the sediment binding and water clarifying characteristics of the habitat are destroyed.

In a more detailed study, Posidonia spinosa was shown smothered by dense epiphytic fouling caused by eutrophication. Transplants of healthy Posidonia shoots from unpolluted to polluted areas resulted in rapid fouling by algae causing death while similar transplants into unpolluted waters remained healthy (Cambridge, 1979). It was concluded that the major effect of eutrophication on macrophytes was indirect by enhancing epiphyte growth and plankton biomass, thereby reducing available light. Cambridge (1979) further discussed the implications of particulate matter in the water column to macrophytes. She stated that, "If particles are suspended through the water column, the seagrass meadow will contract vertically, as plants die at the deeper limit. However, if particles such as silt or algae coat the leaves consistently over a time, then plants are likely to die throughout the depth range depending more on the density of the coating than the incident light intensity." Thus, epiphytic fouling and the accumulation of material on seagrass leaves can be enhanced by increased nutrients and ultimately cause the destruction of the host plant.

In estuarine systems which are becoming increasingly enriched with nutrients, not only epiphytic fouling but also phytoplankton production would increase. This would result in more light stress on the seagrasses and, eventually, if severe enough, would totally eliminate the plants. If periphyton grazers of seagrass habitats decline in abundance while periphyton and/or phytoplankton populations increase, seagrass productivity may decline even more rapidly than in systems where periphyton grazing is not important. Unfortunately, a complete understanding of many of these complex interactions are still undetermined and await future research by the scientific community.

V. MANAGEMENT IMPLICATIONS

Seagrasses are natural resources which by serving multiple functional roles substantially increases coastal zone productivity. The value of submerged vegetation can be expressed in ecological (productivity, habitat complexity), aesthetic (bird watching), recreational (hunting, fishing, crabbing) or economical terms (contributions to a commercial fishery) and when compared to that of nonvegetated habitats the value of grassbeds is considerably higher.

Human activities such as industrialization, development of coastal areas because of recreational appeal, agricultural land usage and dredge and fill operations are increasing in many parts of the world. Such activities have lead to well documented declines of seagrass beds in both temperate and tropical areas (Taylor and Saloman, 1968; Maggi, 1973; Cambridge, 1975, 1979; Peres and Picard, 1975; Zieman, 1975, Larkum, 1976).

Natural perturbations such as hurricanes, diseases, overgrazing and the rapid encroachment of sand waves can also be responsible for seagrass declines although they do not seem to be as widespread as man-induced changes (Cottam, 1934; Cottam and Munro, 1954; Camp et al., 1973; Patriquin, 1975; Zieman, 1976; Kirkman, 1978).

Two of the major results of human activities that appear to be correlated with seagrass declines are to decrease water transparency and to increase nutrients, thereby enhancing epiphytic growth. Although examples of causal factors from detailed field and laboratory experiments are few, there is a growing body of information that focuses on nutrient enrichment of coastal waters (Neilson and Cronin, 1981). Since numerous undesirable effects of eutrophication such as red tide outbreak, the production of noxious odors, and the occurrence of fish kills caused by lowered dissolved oxygen levels have been documented in addition to declines of seagrasses, emphasis is being placed on reducing both point and nonpoint sources of pollution with a goal towards improving land management practices.

Managers face a difficult task in striking a balance between recreational, industrial, agricultural and ecological uses of a watershed. When making ecologically related decisions land managers must be fully aware of the complexities and natural variations that occur within a particular ecosystem and how these factors might be influenced by human induced perturbations. Reducing nutrient loading in coastal areas may be exceedingly difficult, if not impossible, particularly if management strategies require exorbitant funding. However, when the overall contribution to the economy of an area by valuable habitats such as beds of submerged vegetation is assessed, the alternatives to inadequate management may be more economically desirable overall. Adoption of good land use practices to reduce or eliminate nutrients in the watershed as well as strict enforcement of these procedures may ultimately be the most desirable choice of alternatives for the economy and welfare of future generations.

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CHAPTER 2

THE EFFECT OF SALINITY STRESS ON THE SURVIVAL AND BEHAVIOR OF *BITTIUM VARIUM* ADULTS AND LARVAE

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ABSTRACT

The effects of salinity reductions on the activity and survival of Bittium varium adults and larvae were examined under laboratory conditions. Five salinity tests, three tests using adults and two tests using newly hatched larvae were conducted by either rapidly or gradually reducing the salinity. The results of the tests showed that salinities lower than 10 $^{o}/oo$ are stressful for adult B. varium. Adult B. varium died at 6.9 $^{o}/oo$ when exposed to a rapid reduction in salinity. With a gradual reduction, they survived to 6.9 $^{o}/oo$ but individuals were sluggish in their behavior. Veliger larvae were more susceptable to salinity stress than adults. Larvae did not survive in salinities of 11 $^{o}/oo$ while some development occurred between 11 and 16 $^{o}/oo$. However, metamorphosed individuals were found only at 22 and 16 $^{o}/oo$.

The greater susceptability of larvae to salinity reductions compared to adults suggests that the loss of B. varium from western shore grass beds following Tropical Storm Agnes in June 1972, may have been due to reduced or no recruitment during peak spawning periods. The virtual absence of juveniles in these beds late in 1972, further substantiates this hypothesis. Loss of B. varium and alterations of the grazer populations in many of these areas may have important implications for the decline of eelgrass in these areas since the passage of Tropical Storm Agnes.

INTRODUCTION

The eelgrass (*Zostera marina* L.) epifaunal community in the Chesapeake Bay is a diverse assemblage of species from numerous taxonomic groups, e.g. hydrozoans, nemerteans, amphipods, isopods, polychaetes, gastropods, nudibranchs, cirripeds and bivalves (Marsh, 1973, 1976). Functionally, it comprises herbivores, carnivores, and omnivores.

One numerically dominant herbivorous gastropod, *Bittium varium* Pfeiffer (Cerithiidae), is the subject of the present study. Found in densities of up to 200 individuals per gram of eelgrass (Marsh, 1976), *B. varium* may be an important consumer. Experiments with *B. varium* grazing on eelgrass periphyton showed that leaves with *B. varium* had 63% dry weight less periphyton than leaves without *B. varium* (van Montfrans et al., 1982). This grazing action may have important implications for the distribution of eelgrass, especially for those plants living in habitats where light levels reaching the plant surface may be only marginally adequate for photosynthetic maintenance (van Montfrans et al., 1982).

In June 1972 a major hurricane (Tropical Storm Agnes) affected the Chesapeake Bay. The extensive rainfall that accompanied Agnes rapidly and drastically reduced salinities Baywide, especially in surface waters in the western portion of the Bay and its tributaries (Davis and Laird, 1977). Adult *B. varium* were observed in the York River soon after Agnes in July and August 1972 but juveniles, normally present in the population at this time, were not (Orth, 1977, and pers. obs., 1972). Juveniles normally replace adults in the population by late summer so that *B. varium* present each breeding season are those produced the preceding season (unpublished data). Surveys of the eelgrass epifauna in 1973 revealed relatively few *B. varium* in waters along the western shore of the Bay where they had been abundant before Agnes, suggesting that the 1972 year class may have been detrimentally affected by the salinity reduction (Orth, 1977). Since the storm occurred during the time *B. varium* reproduces, it was hypothesized that it may have somehow interfered with breeding success or increased juvenile mortalities.

Between 1972 and 1974 eelgrass in some areas of the Chesapeake Bay also declined dramatically (Orth, 1976; Orth and Moore, 1982). The decreased abundance of *B. varium* in 1973, and the subsequent coincidental decline of eelgrass in 1973 suggested a causal relationship. It was hypothesized that much reduced *Bittium varium* populations may have been ineffective in grazing periphyton from eelgrass leaves resulting in increased periphyton biomass which was thought to have been detrimental to the eelgrass in this observed decline (van Montfrans et al., 1982).

The studies described herein are designed to study the effects of salinity reductions on Bittium varium adults and larvae and to preliminarily assess the consequences of such reductions for B. varium activity and survival under experimental conditions. Based on an analysis of data from experimental work, the effects of Tropical Storm Agnes on B. varium populations in the lower Chesapeake Bay were re-evaluated in light of the declines of Zostera marina over the last decade.

MATERIALS AND METHODS

Bittium varium used in this study were collected from a natural population occurring with eelgrass near Vaucluse Shores on the Chesapeake Bay side of the Eastern Shore of Virginia (37°25'N latitude, 75°59'W longitude). The eelgrass bed in that area represents one of the largest (140 hectares) and most persistent beds on that shore (Orth et al., 1979). Eelgrass is found there from mean low water (MLW) where it occurs with wideongrass, Ruppia maritima, to a depth of 1.5 m where it occurs in monospecific stands.

Collections were made on eight dates: May 4, 1981; May 20, June 9, June 17, July 9, August 26, October 15 and January 6, 1982. Two methods of sampling were used. In the first, a fine mesh net (0.5 mm) attached to a D-frame sled was pulled through the eelgrass bed. Net contents were sieved to separate Bittium varium from the rest of the material. These snails were immediately transported to the laboratory in coolers (70 l.) and placed in a large holding tank (1360 liters) with flow-through York River water. The salinity of the water at the collecting site and at the laboratory on the York River were similar (22-24 $^{o}/oo$). Mean temperature in the holding tank in June, when adult B. varium were removed from use in Tests 1, 2, and 3, was 26.4°C. Browse for the B. varium consisted of the abundant periphyton that grew either on the walls of the holding tank or on large pieces of the alga, Ulva lactuca, collected in the shoal areas near the laboratory.

In the second method, eelgrass with attached Bittium varium was hand clipped near its base and placed in fine mesh (0.5 mm) collecting bags. These bags were placed in buckets with water and returned to the laboratory. The eelgrass leaves were gently washed to remove B. varium which were either preserved in an alcohol solution and measured at a later date or placed in the holding tank. All B. varium that were collected were used either in the laboratory experiments or in growth estimates.

Before each experiment, a sample of Bittium varium was removed from the holding tank. The length of each snail was measured from the apex of the shell to the lip, to the nearest 0.01 mm using Wild M-3 dissecting stereomicroscope with an ocular micrometer, and the average length of the tank population was determined. Enough *B. varium* for a test were then removed from the holding tank. The correct number for each bowl were counted and temporarily placed in small jars of York River water prior to being gently transferred to each bowl when the test was initiated.

Estimating Bittium varium Growth from a Natural Population

At each sampling period, a number of *Bittium varium* (15-350 depending upon their availability) were randomly chosen from samples collected primarily by the second method. Individuals were measured as described above. Numbers of *B. varium* occurring in 0.50 mm size class categories were tabulated. These categories corresponded to those used in previous work with *B. varium* (Marsh, 1970, 1976).

Bittium varium larvae for salinity tolerance tests were laboratory reared and were obtained from egg masses deposited on pieces of live *Ulva lactuca* and glass plates placed in the holding tank. Egg masses were placed in two 38 liter aquaria with bag filtered York River water (22 °/oo salinity) on 13 July 1981. Veliger larvae were first observed in both aquaria on 15 July. Larvae were fed daily with several milliliters of cultured phytoplankton consisting of *Monochrysis lutheri*, *Isochrysis galbana*, *Pseudochrysis paradoxa*, *Chlorella* sp. and *Tetraselmis suecica* grown in filtered (0.1 μ and 1.0 μ) pasteurized York River water (approximately 22 °/oo).

Aquaria water for the tests of salinities less than 22.4 °/oo was made by diluting bag-filtered water from the York River with appropriate amounts of deionized water. Initially, large volumes of test solutions were made and stored in 48 liter carboys to insure sufficient supplies for water changes throughout the course of the test. Carboys were stored at room temperature (approximately 26°C), similar to that of the incubators and the holding tank. All salinity samples were analyzed using a Beckman Induction Salinometer, Model RS-7B, calibrated with standard sea water (35.00 ± .01 °/oo S) at laboratory temperature. Samples were brought to approximate laboratory temperature and read in duplicate.

Randomly placed finger bowls were maintained in three Precision dual programmed incubators, Model 815. Lighting provided by a bank of fluorescent lights along the length of the door simulated natural diurnal conditions in onset and length of daylight hours. Incubators were programmed to provide a temperature of 24 ± 2°C.

Salinity Tolerance Test 1 - Effect of Rapid Salinity Reduction and Return to Ambient Salinity on Adult Activity and Survival

The first salinity test was designed to study effects of rapid salinity reduction on adult activity and survival. Active snails were considered to be those which were able to adhere to any surface of a bowl and were capable of locomotion. Inactive individuals were those that were retracted or extended but not able to adhere to the glass. Because of the inherent difficulty of determining mortality in snails in the "inactive" category, especially in retracted or immobile individuals, a determination of survival was made only at the termination of the test after snails had been returned to ambient (22.4 $^{o}/oo$ salinity) water. Those snails still inactive after 72 hrs in 22.4 $^{o}/oo$ salinity water were considered to have died. Four salinities were tested: 1.7, 6.9, 10.8, and 22.4 (ambient). Chemically clean glass finger bowls (18 cm x 6.5 cm deep), each with 1200 mls of test water were used as aquaria. There were nine replicates of 22.4, 10.8, and 6.9 $^{o}/oo$ water and three replicates of 1.7 water. Air was continuously pumped to each bowl through capillary tipped pipettes. Each bowl was covered with plastic wrap to reduce evaporation.

Glass plates (7.6 x 12.7 cm) covered with periphyton were introduced to each bowl as a food source for Bittium varium during the test. The plates had been taped to bricks and placed in an existing eelgrass bed to become fouled. Prior to each test, plates were brought to the laboratory, removed from bricks, and suspended horizontally in each experimental bowl approximately 2.5 cm above the bottom by monofilament threads. One hundred B. varium, average length 3.7 mm (N=150), were then gently transferred onto each plate and bowls were placed in incubators.

At 24, 48 and 72 hours, Bittium varium in all bowls were examined using a dissecting stereomicroscope at 6.4X magnification and categorized as either active or inactive. After the 72 hours examination, a salinity sample was taken and water in each bowl was replaced with 22.4 $^{o}/oo$ York River water. Snails were examined after an additional 72 hours.

Salinity Tolerance Test 2 - Effect of Rapid Salinity Reduction on Adult Activity

Because the results of the first test showed a large difference in survival between snails in 6.9 and 10.8 $^{o}/oo$ salinity water, a second test was designed to further examine intermediate salinity tolerances with one control salinity. Nine replicates of 21.3, 11.3, 9.2, and 6.9 $^{o}/oo$ salinity water were tested with 50 Bittium varium, average length 3.9 mm (N=50), in each finger bowl. Methodology was similar to Test 1 except that plastic petri dishes (90 x 15 mm deep) fouled with periphyton were used instead of glass plates. Observations of the snails were made every 24 hours for 12 days using the same criteria as in Test 1. Water in each bowl was changed after 96 and 216 hours with clean water of the original salinity. At this time a sample of the old water from each bowl was taken for salinity determination. Additional food for B. varium was added to the petri dishes by scraping periphyton from the walls of the holding tanks, sieving and concentrating the material, and placing a small portion (approximately 2 mls) in the dish. The test was terminated at 264 hrs and a sample of water from each bowl was taken for a final salinity determination.

Salinity Tolerance Test 3 - Effects of a Gradual Salinity Reduction on Adult Activity

This experiment was designed to test the activity of *Bittium varium* under gradual salinity reductions. Fifty adult *B. varium*, average length 4.0 mm (N=149), from the holding tank were initially placed in each of three bowls with York River water (21.9 ^{o}/oo salinity). Plastic petri dishes fouled with periphyton were used as in Test 2. Every 24 hours *B. varium* were counted and examined for activity using the same criterion as in Test 1. Water in each bowl was then replaced with water of a lower salinity. On five consecutive days salinity was reduced from 21.9, 15.4, 11.3, 9.2 to 7.3 ^{o}/oo, respectively. *B. varium* remained in the 7.3 ^{o}/oo salinity water for 14 days, at which time it was replaced with water of 3.4 ^{o}/oo salinity for an additional 6 days. Snails were observed and counted periodically. Water was changed regularly and food added daily following the procedures described for Test 2.

Salinity Tolerance Test 4 - Effect of Rapid Salinity Reduction on Larval Survival and Metamorphosis

Three salinities were used in this experiment, 22.3, 11.1 and 6.6 ^{o}/oo, with three replicates per salinity. Small finger bowls (11.5 cm in diameter x 4.5 cm deep) were filled with 200 ml of water of the appropriate salinity. Methodology for handling the finger bowls was similar to Test 1.

The test began on 7/20 when veliger larvae hatched since 7/15 were concentrated by siphoning water from the two hatching aquaria (see Methods) through a 35 μ mesh sieve held in a water bath to cushion the larvae. Larvae were rinsed into a 500 ml graduated cylinder and brought up to 500 ml volume with 22.3 ^{o}/oo salinity York River water. The mean number of live larvae per ml (24) was determined from five counts using a Sedgewick-Rafter cell. Water in the cylinder was gently stirred, and one ml was transferred to the cell with a 1 ml volumetric (TD) pipette. One drop of dilute Clorox was added to the cell to kill the larvae which were subsequently counted. The remaining water and larvae in the cylinder were gently stirred before approximately 10 mls (i.e. 240 live veliger larvae) were transferred to each finger bowl with a 10 ml volumetric (TD) pipette. Bowls were then placed in the incubators. Thereafter water was changed periodically (after observations were completed) to new water of the same salinity. Larvae were retained by screening through a 35 μm sieve. Treatment was the same for all bowls on a given day. The larvae were fed daily with several mls of appropriate dilutions of the stock algae culture (described in the Methods section) in order to avoid altering the salinities in the bowls. Dilutions were made with deionized water. The volume of a dilution added to each bowl was adjusted so that all bowls received approximately equal amounts of algae. At each feeding the addition of algal culture to the test bowls was as follows: 2 ml of undiluted stock culture (approximately 22 ⁰/oo salinity) was added per bowl at 22.3 ⁰/oo salinity; 4 ml of a 1 part stock culture to 1 part deionized water dilution (approximately 11 ⁰/oo salinity) per bowl at 11.1 ⁰/oo salinity; and 8 ml of a 3:1 dilution (approximately 6 ⁰/oo salinity) per bowl at 6.6 ⁰/oo salinity. Dilutions of the stock culture were checked before addition to bowls to insure viability of algae. Bowls were monitored fro the presence of viable larvae, either veligers or pediveligers, using a dissecting microscope as in Test 1 beginning on 7/21, one day after larvae were introduced to bowls. Metamorphosed individuals were counted in each bowl and a total compiled at the termination of observations. Observations on a given bowl were terminated when viable larvae were no longer present: the test ran for 17 days.

Salinity Tolerance Test 5 - Effect of Gradual Salinity Reduction on Larval Survival and Metamorphosis

Effects of five salinities (22.3, 16.3, 11.1, 9.5, and 6.6 ⁰/oo) with six replicates per salinity were studied. This test was initiated and run concurrently with Test 4. Initially, small finger bowls were set up with 200 ml of 22.3 ⁰/oo salinity water in six bowls and 200 ml of 16.3 ⁰/oo salinity water in 24 bowls. Using the techniques described in Test 4 approximately 240 veliger larvae in 10 ml of 22.3 ⁰/oo salinity water were transferred to each of the 30 bowls. After each 24 hour period all water was changed. The technique for changing water was the same as in Test 4. Bowls with 22.3 ⁰/oo salinity remained at that salinity while six of the 24 bowls with 16.3 ⁰/oo salinity were kept at 16.3 ⁰/oo and the remaining 18 bowls were filled with 11.1 ⁰/oo salinity water. This procedure was followed again at 48 and 72 hours with six bowls remaining at the lowest prior salinity and all remaining bowls changed to the next lowest salinity. After 72 hours, 6 bowls remained at 6.9 ⁰/oo, the lowest salinity being tested. Larvae were fed daily following the procedure described in Test 4. Prior to each water change, 6 bowls were examined under a dissecting microscope for presence of viable larvae, either veligers or pediveligers. Metamorphosed individuals were counted in each bowl and a total compiled at the termination of observations. Observations on bowls with 11.1, 7.5 and 6.6 ⁰/oo salinity were terminated on 7/29. Those on 16.3 and 22.3 ⁰/oo were terminated on 8/7. Periodic salinity samples were taken. The test continued for 17 days until all larvae had either died or metamorphosed.

RESULTS

Bittium varium Growth

Of the initial May 5, 1981 sample of Bittium varium from Vaucluse Shores, 56% were between 2.50-2.99 mm in shell length while 89% were between 2.50 and 3.49 mm (Fig. 1). The tendency for the population to

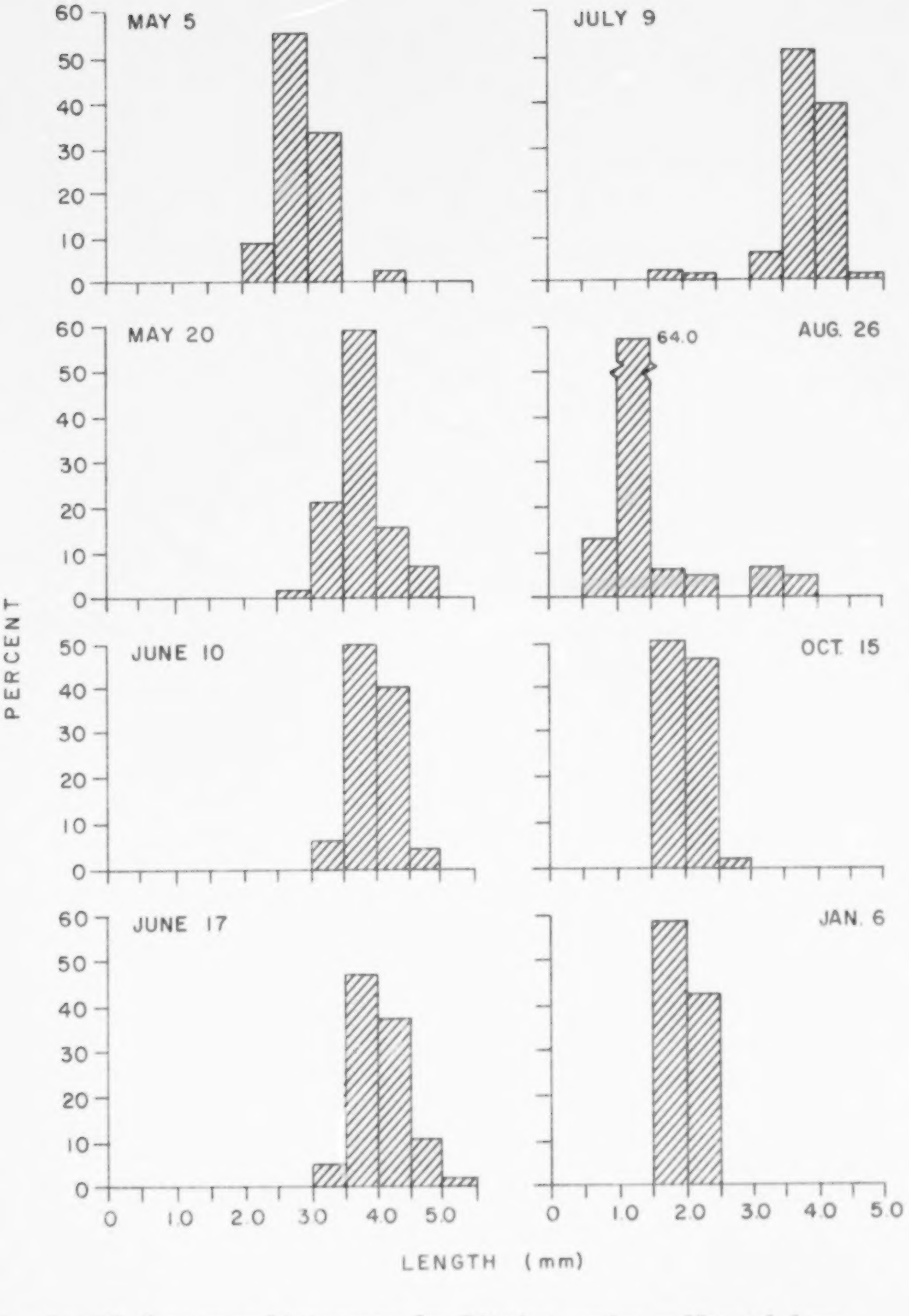

Figure 1. Length-frequency histograms for Bittium varium collected from Vaucluse Shores from May 5, 1981 to Jan. 6, 1982.

be distributed in one or two size classes was evident in all eight sampling periods indicating not only synchronous growth but evidence of distinct year classes. By June 10, 1981, 90% of the individuals were between 3.50 and 4.49 mm shell length. One week later the largest individuals were recorded with 11% of all individuals between 4.50 and 5.49 mm. On August 26, the new year class was evident with 77% of the individuals between 0.50 and 1.49 mm and with a notable reduction in the larger size class categories that were abundant previously. On October 15 and January 6, 98-100% of the individuals were between 1.50 and 2.49 mm with the absence of individuals greater than 3.00 mm. There appeared to be little growth of *B. varium* between October 15 and January 16 as there was no significant difference in the percentage of individuals in the size class represented.

Salinity Tolerance Test 1

Table 1 presents the results of the first salinity tolerance test in which *B. varium* (average length 3.7 mm, n=150) were exposed to a rapid salinity reduction. There were no active *Bittium varium* in the 1.7 ^{o}/oo salinity after 72 hrs or after snails were placed back in 22.4 ^{o}/oo water for 72 hours. At the 6.7 ^{o}/oo salinity, only a few survived while at the 10.8 and 22.4 ^{o}/oo salinities, 100% were active after 24 hours with only 1-2 described as not active after 72 hours. There were no differences in the percentages of active snails at these two latter levels. The major result in this test was the significant difference ($p<0.05$) in survival of snails at the 6.7 and 10.8 ^{o}/oo salinities.

Salinity Tolerance Test 2

Table 2 presents the results of the second salinity tolerance test in which *Bittium varium* (average length 3.9 mm, n=50) were exposed to a rapid salinity reduction. Shown is the mean percentage of active snails for each salinity interval every 24 hours, and also salinity tests representing subsets with means that are not significantly different ($p>0.05$, one-way ANOVA with a Student-Newman-Keuls test for significant differences among the means; all tests were performed on arc-sine transformed data. Almost no snails were active in the 6.9 ^{o}/oo salinity after the first 24 hours. The numbers of snails active at this salinity were signifiantly less ($p<0.05$) than those active at the other salinities. The mean percentage of active snails at the 9.2 ^{o}/oo salinity was always significantly greater ($p<0.05$) than the 6.9 ^{o}/oo salinity but significantly less ($p<0.05$) than the mean percentage of active snails in 11.3 and 21.3 ^{o}/oo salinities (except at 144 hours, when the 9.2 and 11.3 ^{o}/oo salinities were not significantly different, $p>0.05$). There was no significant difference ($p>0.05$) in the mean percentage of active snails between the 11.3 and 21.3 ^{o}/oo salinities. Table 3 presents mean salinity and standard deviation at 96, 216, and 264 hours for four of the test salinities.

TABLE 1. THE MEAN PERCENT AND STANDARD DEVIATION OF ACTIVE SNAILS IN EACH TEST AFTER 24, 48 AND 72 HOURS AND THE % SURVIVING AFTER BEING PLACED IN AMBIENT SALINITY (22.4 %) FOR AN ADDITIONAL 72 HOURS. NUMBERS IN PARENTHESIS AFTER TEST SALINITY INDICATE NUMBERS OF REPLICATES FOR THAT TEST. MEAN SALINITY AND STANDARD DEVIATION AT FIRST 72 HOURS FOR FOUR TEST SALINITIES ARE GIVEN.

Test Salinity	% Active and S.D.			Mean Salinity and S.D. at 72 hrs	72 hrs. in 22.4 ^{o}/oo
	24 hrs	48 hrs	72 hrs		
1.7 (3)	0±0	0±0	0±0	2.2±0.3	0±0
6.7 (9)	0.8±0.9	1.4±2.1	1.4±2.2	7.4±0.1	0.8±1.6
10.8 (9)	100±0	100±0	99.9±0.3	12.8±0.6	98.2±2.3
22.4 (9)	100±0	100±0	99.9±0.3	24.4±0.7	99.7±0.5

TABLE 2. THE MEAN PERCENT OF ACTIVE SNAILS IN EACH SALINITY TEST (n=9) EVERY 24 HOURS FOR 288 HOURS. NUMBER IN PARENTHESIS GIVES PERCENT ACTIVE SNAILS AND HORIZONTAL LINES BELOW THE SALINITIES INDICATES HOMOGENOUS SUBSETS WHOSE MEANS ARE NOT SIGNIFICANTLY DIFFERENT ($p>0.05$).

Time (hrs.)	Salinity (mean percent active)			
24	6.9(2.4)	9.2(94.9)	11.3(100)	21.3(100)
48	6.9(0.4)	9.2(92.7)	11.3(100)	21.3(100)
72	6.9(0.9)	9.2(92.7)	11.3(100)	21.3(100)
96	6.9(1.1)	9.2(93.3)	11.3(96.4)	21.3(99.8)
120		9.2(91.8)	11.3(96.0)	21.3(99.8)
144		9.2(91.8)	11.3(91.8)	21.3(99.8)
168	Terminated-	9.2(92.0)	11.3(96.0)	21.3(99.3)
192	snails	9.2(93.6)	11.3(95.3)	21.3(100)
216	decayed	9.2(93.1)	11.3(95.3)	21.3(99.3)
240		9.2(91.1)	11.3(95.3)	21.3(99.6)
264		9.2(90.9)	11.3(95.6)	21.3(98.9)
288		9.2(74.4)	11.3(95.2)	21.3(99.8)

TABLE 3. MEAN $^{o}/_{oo}$ SALINITY AND STANDARD DEVIATION AT THE 96, 216, AND 264 HRS FOR THE FOUR TEST SALINITIES.

Test Salinity	Mean Salinity ± S.D.		
	96 hrs (6/19)	216 hrs (6/24)	264 hrs (6/26)
6.9	7.4 ± 0.2	--	--
9.2	9.8 ± 0.3	10.0 ± 0.2	9.5 ± 0.1
11.3	12.1 ± 0.3	11.8 ± 0.5	11.6 ± 0.1
21.3	22.0 ± 0.3	22.4 ± 0.3	22.3 ± 0.1

Salinity Tolerance Test 3

The results of Test 3 indicated there was no significant difference ($p>0.05$; one-way ANOVA) in the daily percentage of active snails from the start of the experiment until 456 hours later, one day after they were placed in 3.4 ^{o}/oo salinity water (Table 4). Data from the last 3 observation periods were significantly different from the preceding period, after the snails had been in 3.4 ^{o}/oo salinity water for more than 24 hours. A one-way ANOVA of percent active snails by salinity indicated a significant difference in the 3.4 ^{o}/oo level ($p<0.05$) from the five other levels which were not significantly different ($p>0.05$).

Salinity Tolerance Test 4

Table 5 presents the results of the number of veliger larvae that metamorphosed at the three salinity levels used in this test. In salinity test 4, metamorphosed individuals were found only in 22.3 ^{o}/oo salinity water. Larvae at this salinity survived up to 17 days after the experiment was initiated when the last metamorphosed snail was recorded. Although no individuals metamorphosed in 11.1 ^{o}/oo salinity water, some larvae in all three bowls did reach pediveliger stage by 7/22. Viable larvae were not observed in 11.1 ^{o}/oo salinity bowls after 7/23. Larvae in 6.6 ^{o}/oo salinity bowls were not alive at the first observation on 7/21, one day after the larvae had been introduced.

Salinity Tolerance Test 5

Larvae metamorphosed and survived after 18 days only in 22.3 and 16.3 ^{o}/oo salinity water in both tests (Table 5) and there was no significant diference between the two salinities ($p>0.05$). Considerable variation was observed among the six bowls at these two salinities with regard to the total number of metamorphosd individuals in both tests.

Observations made during the gradual salinity reduction test(s) indicated that the 11.1 ^{o}/oo larvae were active for 48 hours while at 72 hours larvae were alive but inactive. After 170 hours, all larvae had experienced mortality. Larval development was observed to occur at this salinity as some advanced from the veliger to the pediveliger stage and some had metamorphosed for up to 96 hours after the experiment started, but those which remained at 11.1 ^{o}/oo salinity died soon thereafter. Some Larvae transferred to the 9.5 ^{o}/oo level were still active at 48 hours but at 72 hours all larvae were dead. Larval development was observed to occur at 11 ^{o}/oo salinity as some advanced from veliger to pediveliger stage and one metamorphosed within the first 24 hours but none survived. By the time the larvae were placed in 6.9 ^{o}/oo water the number of larvae were reduced

TABLE 4. PERCENT ACTIVE SANILS AT EACH OBSERVATION PERIOD AND THE SALINITY °/oo AT WHICH SNAILS WERE PRESENT DURING THAT PERIOD. VERTICAL LINES TO THE LEFT OF THE HOURS COLUMN INDICATE SUBSETS OF DATA ON SNAIL ACTIVITY WHOSE MEANS ARE NOT SIGNIFICANTLY DIFFERENT (SNK, $p>0.05$).

Time (hours)	Salinity	Percent Active		
		Bowl 1	Bowl 2	Bowl 3
24	21.9	100	100	100
48	15.4	100	100	100
72	11.3	100	100	98
96	9.2	100	100	100
120	7.3	96	98	98
168	7.3	94	98	100
192	7.3	100	100	100
216	7.3	100	100	100
240	7.3	100	100	100
360	7.3	100	98	100
432	7.3	94	98	96
456	3.4	90	92	94
528	3.4	86	10	78
552	3.4	70	10	84
600	3.4	36	2	52

TABLE 5. TOTAL NUMBER AND MEAN ± 1 S.D. OF METAMORPHOSED *B. VARIUM* OBSERVED PER TEST SALINITY IN THE TWO TESTS WHERE VELIGER LARVAE WERE EXPOSED TO RAPID SALINITY SHOCK (TEST 4) AND A GRADUAL SALINITY REDUCTION (TEST 5) OVER AN 18 DAY PERIOD. ALL TESTS STARTED WITH APPROXIMATELY 240 LARVAE IN EACH BOWL. VERTICAL LINES TO THE LEFT OF THE SALINITY COLUMN INDICATE SUBSETS OF DATA WHOSE MEANS ARE NOT SIGNIFICANTLY DIFFERENT (SNK, $p > 0.05$).

Test 4. Rapid Salinity Reduction
No. of Metamorphosed Ind.

Test Salinity $^{o}/_{oo}$	Number per Bowl			Total Number	Mean No. and S.D.
	A	B	C		
22.3	6	9	1	16	5.0 ± 4.6
11.1	0	0	0	0	0 ± 0
6.6	0	0	0	0	0 ± 0

Test 5. Gradual Salinity Reduction
No. of Metamorphosed Ind.

Test Salinity $^{o}/_{oo}$	Number per Bowl						Total Number	Mean No. and S.D.
	A	B	C	D	E	F		
22.3	3	2	15	2	10	25	57	9.5 ± 9.2
16.3	3	9	13	2	4	6	37	6.2 ± 4.2
11.1	0	0	0	0	0	0	0	0 ± 0
9.5	0	0	0	0	0	0	0	0 ± 0
6.6	0	0	0	0	0	0	0	0 ± 0

although some were still actively swimming. However, after only 24 hours at this salinity, live larvae were no longer present.

DISCUSSION

Based on results of sampling the Bittium varium population at Vaucluse Shores in 1982 as well as results from previous studies (Marsh, 1973, 1976; Diaz et al., 1982), the life span of B. varium is estimated to be approximately 14 to 18 months. B. varium generally reproduces in June, with a new year class appearing in early July. Adults either die after spawning or live for only several months thereafter. By October-November, adults were not found in the Vacluse Shore grassbed. The new year class overwinters in the sediments, continues to grow in the spring and early summer and spawns in late June to complete the life cycle.

Newly hatched, free-swimming veliger larvae emerge from egg cases laid on Zostera marina leaves. They apparently are not released as pediveligers or crawling juveniles. Swimming veliger larvae were observed for periods as long as 18 days in our experimental tests. However, the length of the larval life may actually be much shorter under natural conditions because the presence of Z. marina leaves may induce faster settlement of the larvae. This phenomenon has been observed with planktonic larvae of many other invertebrate species where either the presence of adults of that species or certain sedimentological properties hastens settlement (Wilson, 1948, 1952, 1953, 1954, 1955, 1960, 1968, 1970; Knight-Jones, 1951, 1953; Sheltema, 1961; Bayne, 1965; Thorson, 1966, 1975; Carriker, 1967).

The results of laboratory salinity tests showed that salinities lower than 10 $^{o}/oo$ are stressful for adult Bittium varium. When exposed to rapid salinity reductions, B. varium did not survive 6 $^{o}/oo$ salinity (test 1 and 2). Although there was significant survival at 9 and 10 $^{o}/oo$ salinity, anectdotal notes taken during the tests indicated that there were qualitative differences in the behavior of some of the snails in these levels. Snails moved along the bowls much more slowly and their bodies were less extended from the shells than snails at the 11 and 21 $^{o}/oo$ levels. When dislodged from feeding surfaces, some snails at the 9 and 10 $^{o}/oo$ reattached more slowly than at the higher salinity levels. Some snails at the 9 $^{o}/oo$ level in test 2 appeared to equilibrate to that level and become more active as several had even deposited egg cases in their bowls.

Although in the gradient salinity test (test 3), adults survived at 6.9 $^{o}/oo$, anectodotal observations indicated that their behavior was distinctly different from those in the higher salinities. Snails were barely extended from their shells and moved very slowly. Feeding presumably did not occur initially since fecal pellets were not observed. Although movement was still quite slow after 120 hours in 6.9 $^{o}/oo$ water, some snails began to feed and egg cases were noted in two of the bowls. However, when placed in 3.4 $^{o}/oo$ water, the snails experienced rapid mortality and the few remaining at the end of the experiment showed almost no movement.

The results of the tests using the veliger larvae indicated that larvae were more susceptible to salinity stress than adults. Live metamorphosed juveniles were not observed for extended periods in treatments with salinities less than 11 ^{o}/oo. Observations of larvae in the gradual salinity reduction experiment (test 5) indicated that larvae survived and some development occurred at salinities lower than 16 ^{o}/oo and that several had metamorphosed, although eventually, both larvae and metamorphosed individuals died.

Interpretation of data from salinity tolerance tests using both adult and larval Bittium varium suggests that the reduced salinities following Agnes could have affected B. varium populations by causing larval mortalities. The timing of the passage of Agnes may have been the most critical factor in its effect on the eelgrass fauna, especially B. varium. Assuming that B. varium was reproductive at the time of Agnes, it is likely that the very low salinities in the lower Bay tributaries could have detrimentally affected the recruitment of the new year class. At the mouth of the York River (Sandy Point along the north side), the salinity after Agnes was as low as 9 ^{o}/oo and did not rise above 13 ^{o}/oo until August 8, almost 45 days after Agnes. Normally salinities in the area ranged between 15 and 20 ^{o}/oo for the same period during previous years. Adults were present after Agnes at this site but the juveniles were not observed in samples collected in August (Orth, pers. obs.). Some recruitment and survival of juveniles must have occurred because B. varium were present in samples collected in 1973 at several sites in the York River, but their abundances were lower than levels recorded before Agnes (Orth, 1977).

It is also possible that Bittium varium adults at the Zostera marina beds further upriver suffered greater mortality than downstream populations since salinities were 6 to 6 ^{o}/oo or even lower for at least a week after Agnes. Surviving individuals could have postponed reproduction until a normal salinity level returned. The few experimental snails which survived exposure to 6 ^{o}/oo salinities in Test 5 were observed laying egg cases after being returned to York River water (22 ^{o}/oo).

In summary, although detailed information on biological changes in Zostera marina beds in the lower Bay immediately following Agnes is limited, our data suggest that the dramatic reduction in Bittium varium populations along the western shore of the Bay may be attributable to larval mortality caused by extreme salinity reductions. Bittium varium larvae appear to be more susceptible to mortality by reduced salinities than adults and therefore the very low salinities recorded after Agnes coincidental with the time B. varium reproduces, may have seriously interefered with subsequent recruitment. Since B. varium only reproduces once in the summer and adult mortality occurs shortly after spawning, the population dynamics of this species could seriously be altered by extremely low salinities. A significant reduction of *B. varium*, an important member of the *Z. marina* epifaunal community could subsequently result in a very different epiphyte community structure. If the role of *B. varium* is significant in reducing epiphytic growth thereby ultimately enhancing plant vigor, the loss of *B. varium* following Agnes could have reduced the vigor of *Z. marina* and encouraged the decline of *Z. marina* in 1973, one year after Agnes.

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CHAPTER 3

THE ROLE OF GRAZING ON EELGRASS PERIPHYTON: IMPLICATIONS FOR PLANT VIGOR

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ABSTRACT

Natural periphyton removal through grazing and subsequent effects on the growth of transplanted eelgrass (Zostera marina) were investigated in laboratory microcosms. Experimental treatments contained herbivorous gastropods (Bittium varium) which fed on the periphyton growing on Z. marina under three levels of shading (25, 47, and 63% light reduction) for approximately 30 days. Control tanks were similar but did not contain B. varium. Parameters measured at the termination of the experiment included number of shoots, leaf weight, leaf area, periphyton dry weight and ash-free dry weight, chlorophyll a, phaeophytin a and macroalgal standing crop.

Light attenuation in the three shade treatments was significantly different between treatments. The effects of the presence of B. varium in the tanks were clearly seen within a week after the experiment was initiated. Leaves with B. varium were relatively clean while leaves without B. varium were thickly coated with periphyton. At the end of the experiment, treatments with B. varium at the high and low shading levels had significantly more shoots, greater leaf area and a higher leaf weight than the comparable controls. There was no significant difference in these three parameters across shade levels for both the experimental treatments and the controls. Periphyton and ashfree periphyton weights increased with increasing shading in the absence of B. varium but decreased in the presence of B. varium. Chlorophyll a and phaeophytin a concentrations showed considerable variation at the end of the experiment and were not significantly different among the treatments except at the high shade Bittium treatment for chlorophyll a. Values for phaeophytin a at each shading level tended to be lower in the presence of B. varium than when B. varium was absent.

The results of these experiments have important implications for the growth of the Z. marina and other seagrasses. Production and turnover estimates for marine angiosperms may be closely linked to the degree of periphyton fouling and consequently on the presence or absence of grazers which rely on periphyton as a food source. The absence of B. varium in Z. marina beds along the western shore of the Bay may, in part, be a factor in the decline of these grass beds in 1973.

INTRODUCTION

A recent shift from descriptive to experimental approaches in seagrass studies has helped to elucidate the functional relationships within these complex habitats. Understanding such relationships is crucial to the interpretation of past and present events in localized grassbeds and can also have predictive value. A dramatic decline of *Zostera marina*, a dominant species of submerged aquatic vegetation (SAV) in the more saline portions of the Chesapeake Bay, has occurred since 1972 (Orth and Moore, 1982). Recent research efforts have focused on determining the cause for the decline of SAV species and on understanding the functional role of this important natural resource in the shallow waters of the Bay (Wetzel et al., 1981; Kemp et al., 1981).

The presence of *Zostera marina* adds to the complexity of an otherwise barren sandy bottom and provides food, refuge and substrate for a diverse assemblage of species. The loss or reduction of vegetation drastically reduces species diversity (Orth, 1977) and has even changed the foraging strategy of at least two species of overwintering waterfowl (Munro and Perry, 1981). Many commercially or recreationally exploited species rely either directly or indirectly on seagrasses. Blue crabs (*Callinectes sapidus*) and trout (*Cynoscion* spp.) utilize *Zostera marina* beds as nursery and feeding areas (Heck and Orth, 1980).

Invertebrates inhabiting seagrass beds typically assimilate seagrass-fixed carbon through a bacterially mediated detrital pathway (Fenchel, 1977; Klug, 1980). The infauna and epifauna are in turn fed upon by resident and transient consumers, thus providing a link between the seagrasses and higher trophic levels which frequently contain commercial species (Carr and Adams, 1973; Brook, 1975, 1977; Adams, 1976; Stoner, 1979; Stoner and Livingston, 1980; Zimmerman et al., 1979; Nilsson, 1969; Ryer and Boehlert, 1982; Orth and van Montfrans, 1982; Brown, 1981; Lascara, 1981; Ryer, 1981). The demise of SAV in the Chesapeake Bay may therefore have far reaching effects on numerous local species.

Several factors have been implicated in the decline of seagrasses in the Chesapeake Bay (Stevenson and Confer, 1978). Agricultural land use patterns have resulted in more extensive applications of herbicides and fertilizers, some of which enter the Bay through runoff. Herbicide use has increased with little understanding of its effect on SAV. Nutrient enrichment from both fertilizer runoff and sewage input are known to stimulate plankton productivity resulting in increased turbidity and greater light attenuation, thereby limiting macrophyte growth (Walker, 1959, Rayan et al., 1972; Klausner et al., 1974; Stolp and Penner, 1973). The productivity of both macro- and microepiphytes of seagrasses is also enhanced by nutrient enrichment and the resulting epiphytic proliferation can be a factor in the demise of seagrass beds (Cambridge, 1975; Sand-Jensen, 1977).

A diverse assemblage of epiphytes is typically associated with seagrass blades (Harlin, 1980). Micro-epiphytes (periphyton) are a major food source for many customers inhabiting SAV beds (Kikuchi and Peres, 1977; Harlin, 1980; Ogden, 1980). Grazers of periphyton can substantially reduce the biomass of macro-epiphytes (Hunter, 1980; van Montfrans, et al., in press) thereby possibly mediating the effects of nutrient enrichment on periphyton proliferation. In the absence of grazers, periphyton may have the potential to rapidly overgrow and shade the host plant thus reducing photosynthetic activity (Sand-Jensen, 1977). Borum and Wium-Anderson (1980) determined that heavily fouled _Zostera marina_ leaves received only 10% of the light available for photosynthesis. The wavelength of light absorbed by periphyton growing on _Z. marina_ is identical to that utilized by the host (Caine, 1980). Encrusting diatoms on the leaves of _Z. marina_ therefore utilize almost all of the available solar energy and considerably reduce macrophyte photosynthesis by limmiting both light and bicarbonate uptake (Sand-Jensen, 1977).

Shading experiments have demonstrated the negative effects of light attenuation on plant growth (Backman and Barilotti, 1976; Congdon and McComb, 1979). Because light attenuation is one factor determining the lower depth limit of macrophyte growth, fouling by epiphytes may also affect seagrass distribution (Burkholder and Doheny, 1968; Phillips, 1972; Thayer et al., 1975; Jacobs, 1979; Makai et al., 1980). SAV will decline throughout its depth range when shading by epiphytes results in an inadequate amount of light for photosynthetic maintenance of the host plant (Cambridge, 1975).

In the Chesapeake Bay, _Bittium varium_, a prosobranch gastropod, is one of the dominant grazers on the periphyton associated with _Zostera marina_ (Marsh, 1973, 1976). These small snails (less than _7 mm in shell length_) have been shown to significantly reduce the biomass of periphyton associated with _Z. marina_ under laboratory conditions (van Montfrans, et al., in press). The demise of _Zostera marina_ along the western shore of the lower Bay following the drastic decline of _Bittium varium_ in the same area during 1972 (Orth, 1977) led to the hypothesis that the presence of periphyton grazers can indirectly affect the vigor of the host plant by preventing periphyton proliferation to potentially harmful levels. The objective of this project was to examine how the growth of _Zostera marine_ was affected by the presence or absence of _Bittium varium_ in laboratory experiments.

METHODS AND MATERIALS

Experimental Design

Six large fiberglass tanks (3 x 2 x 0.5 m) each containing nine polypropylene trays (60 cm long x 30 cm wide x 25 cm high) filled to a depth of 14 cm with grassbed sediments were employed in the experiment (Fig. 1). Sediment devoid of vegetation was collected from a Guinea Marsh grassbed at the mouth of the York River one week prior to transplanting the vegetation. Plugs of *Zostera marina* were collected from the same grassbed on 22 May 1981. A cylindrical 30 cm long plexiglass coring tube measuring 9.4 cm in diameter (0.069 m^2 area) was carefully placed around several shoots and pushed into the sediment to a depth of 14 cm. Each plug consisting of eelgrass leaves, roots, rhizomes and attached sediments was placed in a plastic bag after decanting the surplus water and transported to the laboratory in large coolers to prevent desiccation. Six plugs of vegetation were transplanted into each polypropylene tray by removing sediment with the plexiglass core and replacing it with a vegetated plug.

After transplanting the plugs, the fiberglass tanks were filled to 40 cm with ambient seawater from the York River. Thus, the sediment surface in the plastic trays was 26 cm from the air-water interface. York River water was continuously pumped through each tank at the rate of 960 l/hr resulting in a complete turnover every hour.

Tanks were randomly assigned an experimental treatment to test for the effects of three degrees of shading in the presence and absence of *Bittium varium* on plant growth (Table 1). Pairs of tanks were covered with shades reported to reduce ambient light by 25, 47 and 63% (Chicopee brand lumite woven polypropylene shades, style 5187909, 5183809 and 5184009, respectively). The low shade treatment (25% reduction) was chosen to simulate the observed mean light level reaching plants in the Guinea Marsh grassbed during 1979. Medium (47% reduction) and high shade (63% reduction) treatments were designed to reflect further light reductions such as that caused by phytoplankton blooms or increased suspended sediments. A randomly chosen experimental tank under each level of shading was innoculated with *Bittium varium* to test the effects of periphyton grazing on plant growth. The second tank of each pair was designated as the control tank.

Bittium Innoculation

Bittium varium were collected from a large *Zostera marina* bed at the mouth of Hungar's Creek on Virginia's Eastern Shore using a 0.5 meter D-ring epibenthic sled. A standard volume of *B. varium* (1/2 dram = approx. 340 individuals) was introduced to each experimental plug of grass. This was accomplished by lowering the water level in all tanks to 4 cm above the sediment surface, and gently placing the *B. varium* on the *Zostera marina* leaves in the

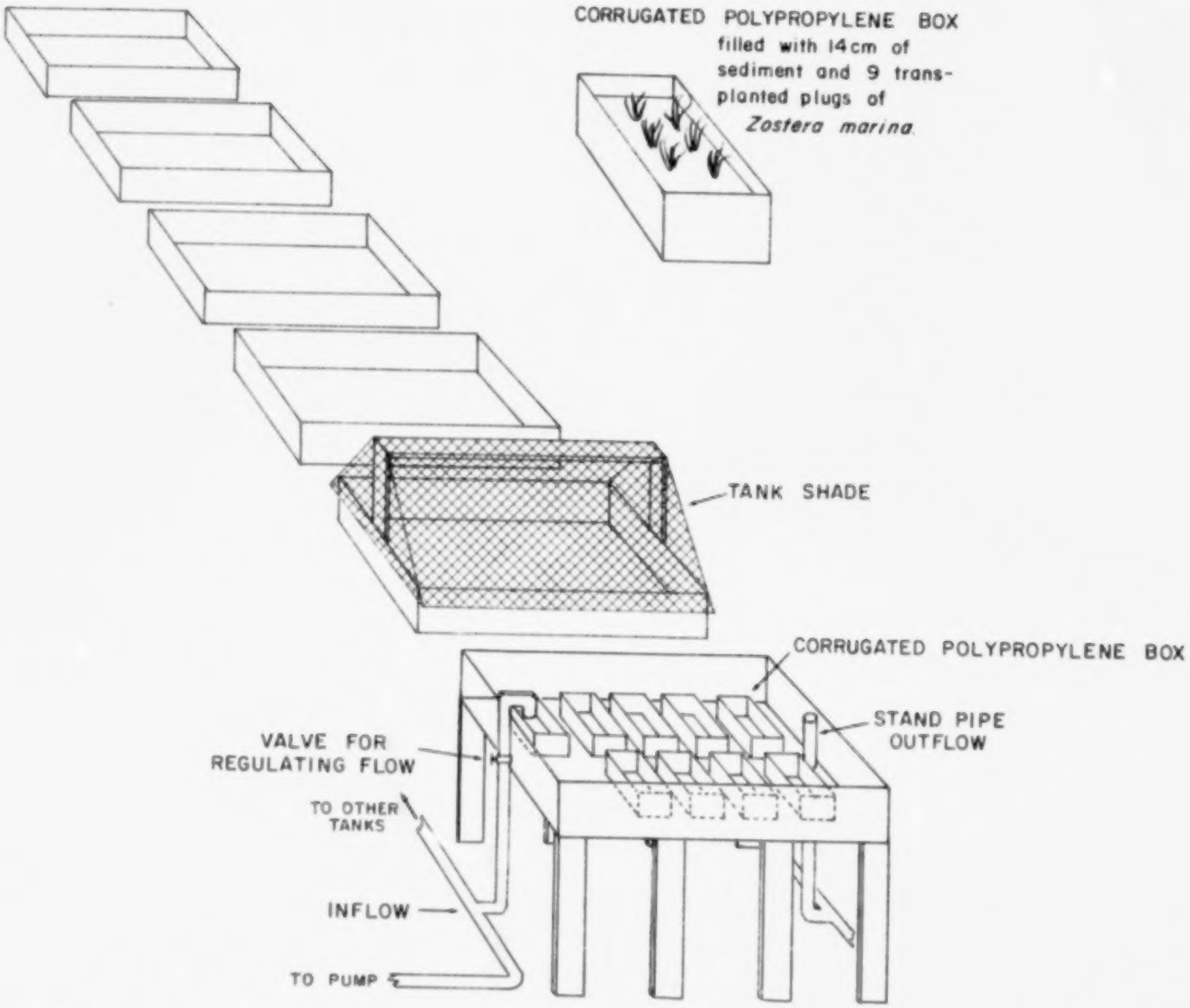
CORRUGATED POLYPROPYLENE BOX
filled with 14cm of
sediment and 9 trans-
planted plugs of
Zostera marina
TANK SHADE
CORRUGATED POLYPROPYLENE BOX
STAND PIPE
OUTFLOW
VALVE FOR
REGULATING FLOW
TO OTHER
TANKS
INFLOW
TO PUMP

Figure 1. Experimental design showing shaded large tanks containing smaller trays with transplanted eelgrass plugs. Ambient York River water was supplied in the flow through design with an input of 960 liters per hour and water levels were controlled by the outflow stand pipe elevation.

TABLE 1. ARRANGEMENT OF TANK EXPERIMENT UTILIZING *BITTIUM VARIUM* UNDER DIFFERENT INTENSITIES OF SHADE.

	Shading	*Bittium*
Tank 1	25%	Yes
Tank 2	63%	No
Tank 3	25%	No
Tank 4	47%	No
Tank 5	47%	Yes
Tank 6	63%	Yes

experimental tanks only. The water in all tanks was then raised to the original level. Snails were first introduced to the plugs on May 22, 1981. Subsequently, we observed that snails soon dispersed to the sides of the tanks and polypropylene boxes when periphyton on grass blades became scarce. Additional snails were therefore placed on experimental plugs on June 4 and June 16.

Tank Cleaning Procedures

All tanks were cleaned on a weekly basis to minimize the rapid fouling of nonliving surfaces. Cleaning was accomplished by lowering the water level in each tank and gently scouring the sides of the tank and polypropylene boxes with a plastic household scouring pad. All algae, barnacles, other encrusting organisms and accumulated sediments were removed by this process. Care was taken not to disturb the transplanted plugs during the 45 minute cleaning procedure for each tank. However, prior to lowering the water level, the water over each plug was agitated uniformly by hand to simulate the wave action that plants frequently experience under field conditions. This was done to remove any loosely adhering particulate material (mostly sediments) that accumulated on the blades due to the reduced turbulence in the experimental tanks.

Sampling Procedure

Sampling was conducted from June 29 through July 3, 1981 approximately one month after initiating the experiment. Three trays with six plugs each were randomly selected from each tank (treatment). While still underwater, shoots of each plug were gently groomed to remove unattached macroalgae and dead grass blades. Next, the shoots of each plug were clipped off at the sediment surface and carefully transferred to an enamel pan filled with seawater. Observations on the number of living shoots, general appearance, and condition of the blades were recorded concurrently. The base of each shoot was then separated from the blades at the leaf node and dried in tared aluminum envelopes for dry weight determinations. The blades were mechanically stripped of all attached periphyton and sediment by being repeatedly drawn through closed forceps. All materials removed in this way remained in the water-filled enamel pans. The stripped blades were saved for leaf area and dry weight determinations.

Bittium varium, if present, were removed from the enamel trays, counted, and preserved in 10% formalin. The remaining contents of the trays were sieved through a 0.5 mm screen and rinsed to force all suspended sediment and microalgae (periphyton) through the screen. The filtrate was collected and stored at 5°C for 16 hrs in 32 oz. jars to allow suspended materials to settle. Excess water was decanted and the contents (i.e. periphyton and sediment) were transferred to 4 oz. jars and frozen for later examination. All materials retained by the sieve were examined under a dissecting microscope to remove all epibiota and *Zostera marina* fragments, leaving only the macroalgae.

The macroalgae were then placed in tared aluminum pans for dry weight determination.

Leaf Area Measurements

Blades from each plug were blotted dry and sandwiched in a flat non-overlapping arrangement between two layers of Saran brand plastic wrap. Grass blade area estimates were then determined using a LI-COR Model LI13100/1+1 Leaf Area Meter. Three area estimates were taken for each plug and from these the mean value was calculated to be the leaf area for that plug.

Chlorophyll a and Pheophytin a Determination

Chlorophyll *a* determinations were made using a modified method developed by Whitney and Darley (1979). This method employs a phase separation technique in which buffered aqueous-acetone extracts are partitioned with hexane to separate interferring chlorophylls and phaeophytin *a* from chlorophyll *a*. The concentration of chlorophyll *a* in the presence of phaeophytin *a* was then detemined from absorbencies of acidified and non-acidified aliquots of the hexane hyperphase read on a Bausch and Lomb Model 21 spectrophotometer at 663 and 750 nm. After pigment extraction of the periphyton samples, all particulates were saved and deposited in tared aluminum pans for dry weight determinations.

Dry Weight and Ashfree Dry Weight Determinations

Dry weights were measured for leaves, shoot bases, macroalgae and periphyton. Materials were dried to constant weight (48 hrs at 50°C in a drying oven), transferred to desiccators for cooling to ambient temperature and weighed on a Mettler balance (Model H-51). After weighing, periphyton samples were combusted in a muffle furnace at 475°C for 4.5 hours, cooled in desiccators, and reweighed.

Light Readings

The actual quantity of light reaching the experimental plugs was determined by taking periodic light measurements using a LI-COR, Inc. Quantum/Radiometer/Photometer Model LI-185B. These were taken both with the shades in place and with the shades removed, at a water depth of 26 cm (the approximate depth of the sediment surface in the trays). Ambient light was also concurrently recorded. Since preliminary analysis showed no significant difference (ANOVA, $p<0.05$) in light attenuation between experimental and control tanks under the same shading regime, subsequent readings were taken in only one of the two tanks for each treatment after the third week.

Ambient light conditions varied from day to day because of weather conditions and therefore all light data are reported as extinction coefficients following the equation:

$$K_d = \frac{-\ln \frac{E_2}{E_1}}{0.26}$$

where

K_d = extinction coefficient
E_2 = light intensity at surface
E_1 = light intensity at 26 cm and
0.26 = depth from surface (in meters).

The data collected for each tank enabled us to test the assumption that light attenuation due to water quality was the same for all treatments, and that observed differences in light intensity were caused by the artificial shades only.

Statistical Analysis

Data gathered from the eighteen replicate *Zostera marina* plugs from each experimental treatment included numbers of shoots, leaf weight, and leaf area. These data were used as primary indicators of plant vigor since they integrated the effects of grazing activity, periphyton fouling and *Z. marina* photosynthesis on plant growth. Direct measurements of periphyton fouling (macroalgae wt., periphyton dry wt. and ashfree wt., chlorophyll *a*, and pheophytin *a*) were also made and standardized as the ratio of the measured parameter to total leaf area per plug.

Data for the sample period were log transformed and tested for homogeniety of variance (Bartletts F-max). In cases where the assumption of homogeneous variance were met, data were analyzed using a combination of one way analysis of variance (ANOVA), Student-Newman-Keuls multiple range testing, and T-test (Sokal and Rohlf, 1969). In cases where variances were determined to be heterogeneous, nonparametric tests were utilized (Kruskal-Wallis one way analysis of variance and Mann-Whitney U-test). Light data were first tested for homogeneity of variance using the Bartlett F-max test, and then analyzed by one way analysis of variance (Sokal and Rohlf, 1969).

RESULTS

Light

The mean quantity of photosynthetically available light (470-560 nm) on sunny days, during the course of the study was 1511 microeinsteins (me). The mean values of light actually available to the experimental plants was 857 me for low shade treatments, 643 me for medium shade treatments, and 452 me for high shade treatments. This represented a 43, 58, and 69% decrease in available light, respectively.

Light attenuation in the three shade treatments (i.e. low, medium and high shade) was significantly different (ANOVA), $p<0.05$) between treatments (Fig. 2; Table 2). With the shades removed, however, no significant differences (ANOVA, $p>0.05$) were observed between tanks (Fig. 3; Table 3) indicating that light differences between treatments were due to the shade covers only. Differences in light between

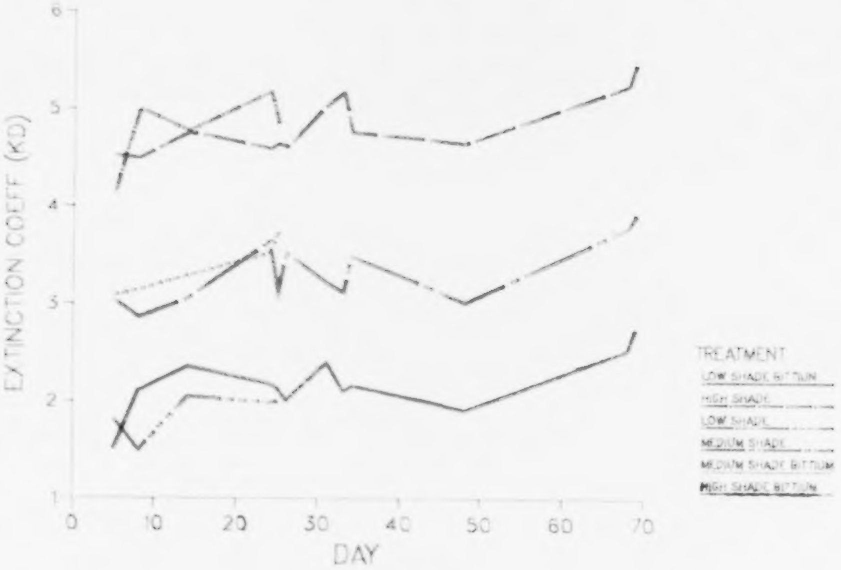

Figure 2. Light attenuation (expressed as the extinction coefficient) in the three pairs of experimental tanks with shades in place. Initially, measurements were made in all six tanks but since paired measurements were not significantly different ($p>0.05$), light measurements after day 25 were taken in only one of each pair of tanks.

TABLE 2. ANALYSIS OF LIGHT ATTENUATION AMONG TREATMENTS (AS MEASURED BY EXTINCTION COEFFICIENTS) DUE TO THE COMBINED EFFECTS OF WATER TURBIDITY AND ARTIFICIAL SHADING.

Analysis of all treatments through day 25 of experiment*

Analysis of Variance (ANOVA)

significant at $p = 0.000$

$F = 50.579$

Student-Newman-Keul (SNK) ($p < 0.05$)

Treatment	L	LB	M	MB	H	HB
Mean Value	1.83	2.19	3.34	3.54	4.62	4.67

Analysis of treatments 1,2, and 3 (low shade *Bittium*, high shade and medium shade, respectively) for entire experiment*

Analysis of Variance (ANOVA)

significant at $p = 0.000$

$F = 75.060$

Student-Newman-Keul (SNK) ($p < 0.05$)

Treatment	LB	M	H
Mean Value	2.19	3.34	4.62

L - Low shade treatment
M - Medium shade treatment
H - High shade treatment
LB - Low shade *Bittium* treatment
MB - Medium shade *Bittium* treatment
HB - High shade *Bittium* treatment
* - On day 25, preliminary analysis (ANOVA) showed the three shading treatment types to be significantly different from one another. However, T-tests demonstrated no significant differences between shading replicates (i.e. *Bittium* vs. non *Bittium*). Therefore it was decided to limit light measurements to one treatment of each shading level for the remainder of the experiment.

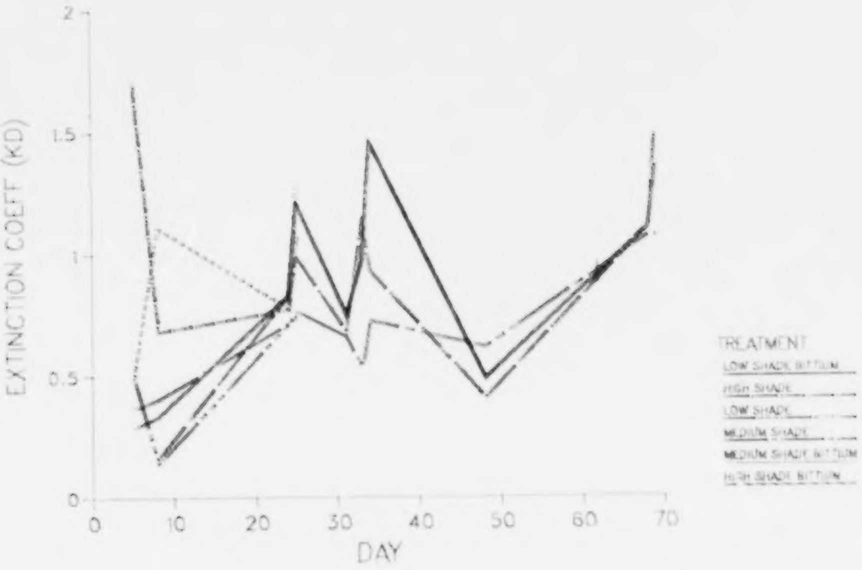

Figure 3. Light attenuation (expressed as the extinction coefficient) in the three pairs of tanks with shades removed. Initially, measurements were made in all six tanks but were not significantly different ($p>0.05$) during the first 25 days and subsequent light intensities were monitored in only one tank under each level of shading.

TABLE 3. ANALYSIS OF WATER TURBIDITY AMONG TREATMENTS (AS MEASURED BY EXTINCTION COEFFICIENTS).

	Analysis of Variance (ANOVA)
Analysis of all treatments through day 25 of experiment*	significant at $p = 0.25$ $F = 1.376$

Student-Newman-Keul Multiple Ranges (SNK) ($p < 0.05$)

Treatment	L	M	H	LB	MB	HB
Mean Value	0.57	0.69	0.77	0.91	0.98	1.06

	Analysis of Variance (ANOVA)
Analysis of treatments 1,2, and 3 (low shade *Bittium*, high shade and medium shade, respectively) for entire experiment*	not significant at $p = 0.46$ $F = 0.788$

Student-Newman-Keul Multiple Ranges (SNK) ($p < 0.05$)

Treatment	M	H	LB
Mean Value	0.70	0.77	0.91

L - Low shade treatment
M - Medium shade treatment
H - High shade treatment
LB - Low shade *Bittium* treatment
MB - Medium shade *Bittium* treatment
HB - High shade *Bittium* treatment
* - On day 25, preliminary analysis (ANOVA) showed the three shading treatment types to be significantly different from one another. However, T-tests demonstrated no significant differences between shading replicates (i.e. *Bittium* vs. non *Bittium*). Therefore it was decided to limit light measurements to one treatment of each shading level for the remainder of the experiment.

experimental (with B. varium) and control (no B. varium) tanks for each of the three shading levels were also not significant (T - test; $p>0.05$).

Plant Vigor: Shoots, Leaf Weight and Leaf Area

Numbers of shoots, leaf weight and leaf area per plug exhibited the same general pattern among treatments (Fig. 4) with experimental treatments being significantly higher for all three variables (ANOVA; $p<0.05$) and with SNK analysis dividing treatments into two respective groups: B. varium present, and B. varium absent (Table 4). Among the two groups there were no significant differences ($p<0.05$) between tanks with different levels of shading. At the high and low shading levels, T-tests ($p<0.05$) showed that treatments with B. varium had consistently higher values for each parameter than did control tanks without B. varium. However, at the medium shade level, T-tests showed that for leaf area and leaf weight, differences were not significant ($p>0.05$) between experimental and control tanks.

Periphyton, Periphyton Ashfree, and Macroalgae Weight

These parameters showed considerable range in their variances, and were therefore analyzed using non-parametric ranking methods. For periphyton and periphyton ashfree dry weights, Kruskal-Wallis one way analysis of variance showed treatments to be significantly different ($p<0.05$) when tested together, as well as when grouped into Bittium and non Bittium categories (Table 5). Examination by the Mann-Whitney U test, showed that control treatments (non Bittum) had consistently higher values when compared to experimental treatments (with Bittum). Thus periphyton and ashfree periphyton weights increased with increasing shading in the absence of Bittium, but decreased in the presence of Bittium (Fig. 5).

With respect to macroalgal weight, all treatments, with the exception of high shading with Bittium, were statistically similar. The latter had a significantly lower mean value (K-W-ANOVA, $p<0.05$) than others.

Chlorophyll a and Phaeophytin a

The variation of chlorophyll a and pheophytin a levels were considerable among treatments. Hence, nonparametric statistical methods were used in data analysis. With respect to chlorophyll a, all treatments were similar, except for the high shade Bittium treatment, which had significantly lower levels of chlorophyll a (K-W-ANOVA, $p<0.05$) (Table 6; Fig. 6). When the ANOVA tested only Bittium treatments, a significant difference among treatments was also observed, with chlorophyll a concentration being inversely related to the level of shading. For phaeophytin, an analysis of variance demonstrated a non-significant variation ($p>0.05$) among all treatments, as well as among the non-Bittium treatment. The Mann-Whitney U test detected a non-significant difference ($p>0.05$)

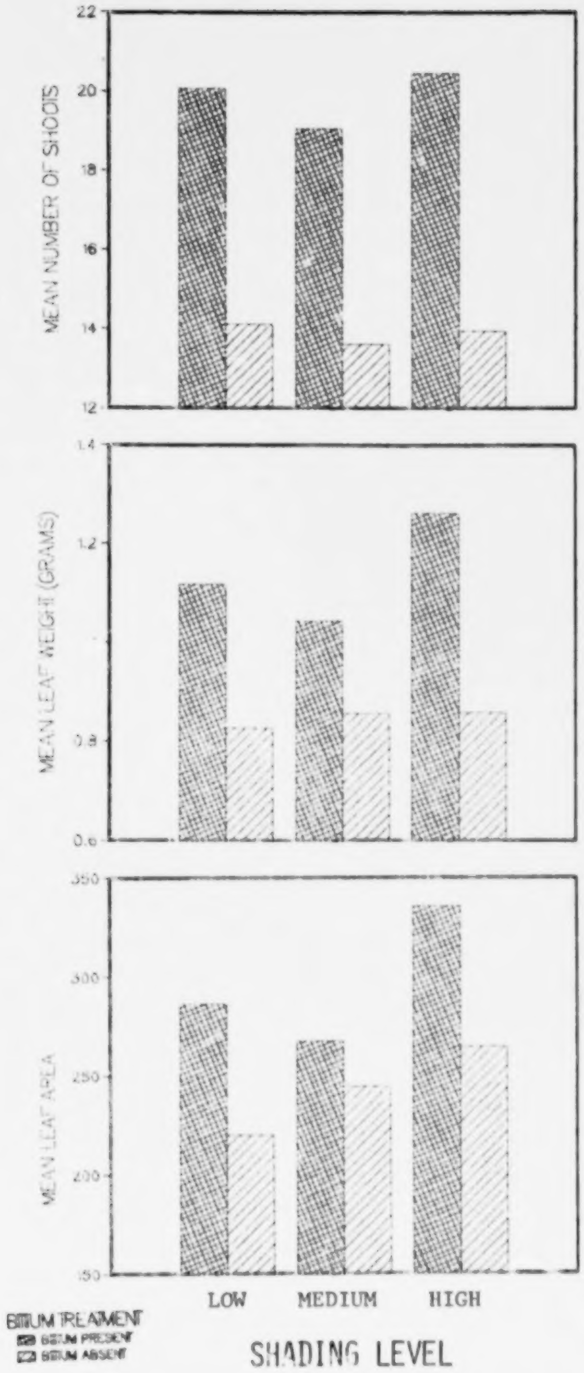

Figure 4. Mean numbers of shoots, leaf weight and leaf area for experimental and control tanks at the three levels of shading.

TABLE 4. STATISTICAL ANALYSIS OF TIME INTEGRATED PARAMETERS MEASURED (NUMBER OF SHOOTS, LEAF WEIGHT AND LEAF AREA DURING THE EXPERIMENT.

	Treatment Groups	Analysis								Significance
Number of Shoots										
	All	ANOVA		F = 7.46						p = 0.000
		SNK	Treatment	M	L	H	MB	LB	HB	p = 0.05
			Mean Value	1.16	1.16	1.17	1.28	1.31	1.32	
	Non *Bittium*	ANOVA		F = 0.05						p = 0.949
		SNK		M	L	H				p = 0.050
				1.16	1.16	1.17				
	Bittium	ANOVA		F = 0.51						p = 0.606
		SNK		MB	LB	MB				p = 0.050
				1.28	1.31	1.32				
	Low shade	T-test		T = 3.84						p = 0.001
	Med shade	T-test		T = -2.73						p = 0.010
	High shade	T-test		T = -4.29						p = 0.000

TABLE 4. (CONTINUED)

	Treatment Groups	Analysis								Significance
Leaf Weight										
	All	ANOVA		F = 5.20						p = 0.000
		SNK	Treatment Mean Value	L 0.26	H 0.26	M 0.27	MB 0.30	LB 0.31	HB 0.35	p = 0.050
	Non *Bittium*	ANOVA		F = 0.11						p = 0.895
		SNK		L 0.26	H 0.26	M 0.27				p = 0.050
	Bittium	ANOVA		F = 1.71						p = 0.19
		SNK		MB 0.30	LB 0.32	HB 0.35				p = 0.05
	Low shade	T-test		T = 2.70						p = 0.011
	Med shade	T-test		T = -1.58						p = 0.123
	High shade	T-test		T = -3.89						p = 0.000

TABLE 4. (CONTINUED)

	Treatment Groups	Analysis								Significance
Leaf Area										
	All	ANOVA		F = 3.34						p = 0.008
		SNK	Treatment Mean Value	L 2.33	M 2.38	MB 2.39	H 2.41	LB 2.42	HB 2.51	p = 0.050
	Non *Bittium*	ANOVA		F = 1.86						p = 0.166
		SNK		L 2.33	M 2.38	H 2.41				p = 0.050
	Bittium	ANOVA		F = 2.56						p = 0.087
		SNK		MB 2.39	LB 2.43	HB 2.51				p = 0.050
	Low shade	T-test		T = 2.29						p = 0.028
	Med shade	T-test		T = -0.28						p = 0.779
	High shade	T-test		T = -2.42						p = 0.021

All data values are log transformed mean values for 18 grass plugs.
L - Low shade treatment
M - Medium shade treatment
H - High shade treatment
LB - Low shade *Bittium* treatment
MB - Medium shade *Bittium* treatment
HB - High shade *Bittium* treatment

TABLE 5. STATISTICAL ANALYSIS OF GRAVIMETRIC DATA FROM THE FOULING COMMUNITY.

Variable	Treatment Groups	Analysis		Significance
Macro Algae Weight	All	K-W	$\chi^2=38.118$	p=0.000
	Non-*Bittium*	K-W	$\chi^2=1.226$	p=0.542
	Bittium	K-W	$\chi^2=30.030$	p=0.000
	Low shade	M-W	U=116.0	p=0.1456
	Med shade	M-W	U=123.0	p=0.2172
	High shade	M-W	U=24.0	p=0.0000
Periphyton Dry Weight	All	K-W	$\chi^2=78.162$	p=0.000
	Non-*Bittium*	K-W	$\chi^2=14.733$	p=0.001
	Bittium	K-W	$\chi^2=18.029$	p=0.000
	Low shade	M-W	U=58.0	p=0.0010
	Med shade	M-W	U=4.0	p=0.0000
	High shade	M-W	U=0.0	p=0.0000
Periphyton Ashfree Dry Weight	All	K-W	$\chi^2=67.353$	p=0.000
	Non-*Bittium*	K-W	$\chi^2=13.194$	p=0.001
	Bittium	K-W	$\chi^2=12.831$	p=0.002
	Low shade	M-W	U=71.0	p=0.0068
	Med shade	M-W	U=9.0	p=0.0000
	High shade	M-W	U=18.0	p=0.0000

All data values are log transformed mean values for 18 grass plugs.
K-W - Kruskal-Wallis oneway ANOVA
M-W - Mann-Whitney U test

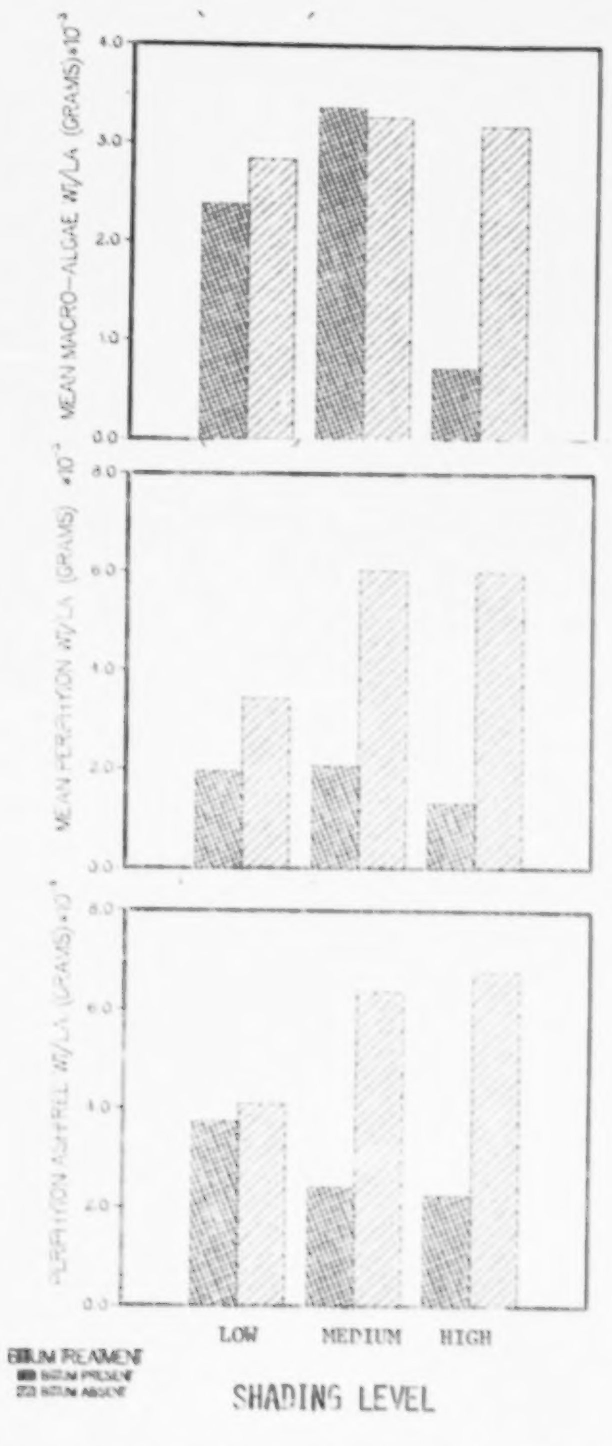

Figure 5. Mean macroalgal weight, periphyton dry weight and periphyton ash free dry weight per leaf area for experimental and control tanks at the three levels of shading.

TABLE 6. STATISTICAL ANALYSIS OF PHYTOPIGMENT DATA FROM THE FOULING PERIPHYTON COMMUNITY.

Variable	Treatment Groups	Analysis		Significance
Chlorophyll *a*	All	K-W	$\chi^2=18.619$	p=0.002
	Non-*Bittium*	K-W	$\chi^2=0.582$	p=0.747
	Bittium	K-W	$\chi^2=24.266$	p=0.000
	Low shade	M-W	U=20.39	p=0.2821
	Med shade	M-W	U=147.0	p=0.6351
	High shade	M-W	U=117.0	p=0.1545
Phaeophytin *a*	All	K-W	$\chi^2=10.611$	p=0.060
	Non-*Bittium*	K-W	$\chi^2=1.004$	p=0.605
	Bittium	K-W	$\chi^2=9.377$	p=0.009
	Low shade	M-W	U=118.0	p=0.1639
	Med shade	M-W	U=117.0	p=0.1545
	High shade	M-W	U=160.0	p=0.9495

All data values are log transformed mean valu for 18 grass plugs.
K-W - Kruskal-Wallis oneway ANOVA
M-W - Mann-Whitney U test

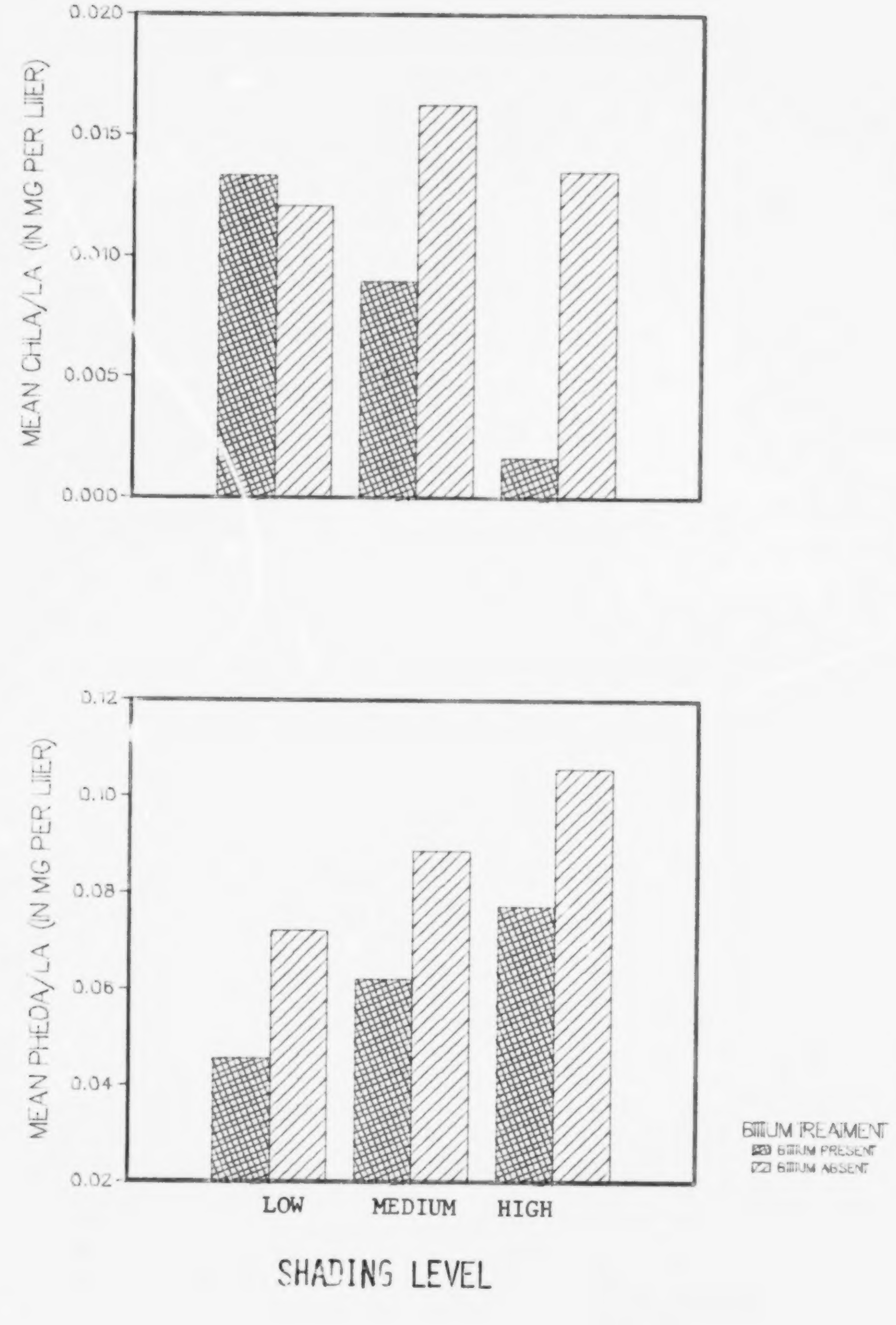

Figure 6. Mean levels of chlorophyll a and phaeophytin a per leaf area for experimental and control tanks at the three levels of shading.

between Bittium and non-Bittium treatments of the same shading levels (Table 6). There appears to be a trend towards a direct relationship between the amount of phaeophytin a present and the degree of shading (Fig. 6) although the observed differences were not statistically different. At each shading level, phaeophytin a levels tended to be lower in the presence of B. varium than when B. varium was absent.

DISCUSSION

Shading of marine angiosperms by epiphytes is a well known phenomenon that has potentially harmful consequences for the host plant (Sand-Jensen, 1977; Borum and Wium-Anderson, 1980). Although some angiosperms possess chemical defenses against various fouling species (Zapata and McMillan, 1979; Harrison and Chan, 1980) the role of micrograzers may be equally or even more important in minimizing fouling.

In our study, measurements of time integrated parameters (leaf biomass, leaf area, and numbers of new shoots produced) provided a clearer indication of periphyton-grazer effects on eelgrass growth than did measurements which were more closely related to the fouling community (periphyton pigment analyses, periphyton dry and ash free dry weight, and macroalgal weight). Experimental tanks (with B. varium) exhibited an inverse relationship between chlorophyll a (high to low) and phaeophytin a (low to high) concentrations under increasing levels of shade. These data imply that under low levels of light and in the presence of grazers, most of the periphyton biomass is nonliving whereas under higher levels of light, the periphyton is living and actively undergoing photosynthesis. These relationships are less apparent in the absence of grazers (i.e. control tanks) suggesting that grazing activity has some influence on the functioning of the periphyton community.

The level of periphyton fouling (microalgae and associated particulates) as measured by dry weight and ash-free dry weight appeared to be related to both the presence or absence of Bittium varium and the level of shading. Periphyton weight is negatively correlated with the level of shading in the presence of B. varium whereas in the absence of B. varium, periphyton weight and shading level are positively correlated (see Fig. 3). Reasons for such relationships remain unclear although it can be suggested that because of the effects of one or both factors, the various treatments have different epiphyte communities.

The level of macroalgal fouling among treatments demonstrated no identifiable relationship with control variables. The only treatment showing significantly different values for this parameter was the high shade Bittium treatments, the reason for which is also not apparent. We have clearly demonstrated over a short period of time that Bittium varium grazing can greatly improve plant vigor based on the time integrated parameters which were measured. Not only did the total Zostera marina biomass increase in the presence of grazers but the fact that a greater number of shoots was produced by the experimental plants indicated that the vegetative reproductive capability of *Z. marina* was enhanced.

Results such as these have important implications for work being conducted in seagrass habitats. Production and turnover estimates for marine angiosperms may be closely linked to the degree of periphyton fouling and consequently on the presence of absence of grazers which rely on periphyton as a food source. Natural or human induced perturbations which alter the structure and composition of micrograzer populations might ultimately determine the distribution and abundance of seagrass beds. Our findings support the contentions of Caine (1980) who suggested that *Z. marina* distribution along the west coast (USA) could be affected by the presence of periphyton grazing amphipods. The elimination of *Bittium varium* from western *Zostera marina* beds in the Chesapeake Bay resulting from reduced salinities during Hurricane Agnes probably contributed to the reduced aerial coverage of eelgrass in the lower Bay.

This idea seems even more plausible if the seasonality of grazer activity, periphyton fouling and *Z. marina* growth is considered. Eelgrass is a perennial plant exhibiting distinct phases of seasonal growth, presumably associated with environmental temperature (Setchell, 1929). In the Chesapeake Bay, *Z. marina* grows slowly during the winter months when water temperatures remain below 6°C. When water temperatures increase to above 10°C during the early spring (March-May) *Z. marina* grows rapidly until temperatures climb above 20°C early in the summer. Growth throughout the summer and early fall months is minimal but is followed by a second, less dramatic period of growth in the late fall (Oct.-Nov.) as temperatures drop. It is during the spring growth peak that eelgrass produces seeds and undergoes extensive vegetative growth. This is also the period of increased epifaunal growth and activity. *Bittium varium* in particular, which recruits late in the summer but remains relatively inactive throughout the cold winter months, grows rapidly as temperatures increase in the spring (Marsh, 1976 and pers. obs.). It is during the important spring months and throughout the summer when fouling and water turbidity are maximal that grazers such as *B. varium* could have their greatest impact on the survival and distribution of eelgrass.

We have shown that under short term experimental conditions, *Zostera marina* exhibits greater growth in the presence rather than absence of the micrograzer, *Bittium varium*. Our results support the hypothesis that recent declines of *Zostera marina* could be related in part to the prior reduction of *B. varium* populations in the lower Chesapeake Bay. The fact that *B. varium* populations and *Z. marina* beds on the eastern shore of the Bay did not experience severe declines after the passing of Hurricane Agnes lends further support to our hypothesis. Future research should focus both on long term experiments to further substantiate our hypothesis and on examining the role of other micrograzers in vegetated habitats.

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